*Bull. nat. Hist. Mus. Lond.* (Ent.) **68**(2): 145–193 Issued 25 November 1999

# A review of the soldierless African termite genus *Amicotermes* Sands 1972 (Isoptera, Termitidae, Apicotermitinae)

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**SYNOPSIS.** The termite genus *Amicotermes* is a member of the soldierless Apicotermitinae (Isoptera, Termitidae), recognised as important constituents of the soil fauna in tropical Africa. Before the current work was begun, 60 species belonging to 16 genera had been recorded, among them the single species from the southern Congo for which the genus was named. New intensive ecological transect sampling in Cameroon and Congo (Brazzaville) by members of the Termite Research Group at The Natural History Museum has greatly increased the observed species diversity of the soil. Eleven new species of *Amicotermes* are keyed and fully described here from a database compiled in DELTA format in PANKEY, which also allows the matrix to be converted to HENNIG86 input or similarity coefficients for phenetic analysis. Phenetic and cladistic analyses of the relationships between the species are provided. All species are illustrated with line drawings and photographic plates.

XX(320629.1)

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## INTRODUCTION

It has been noted before that the soldierless Apicotermitinae (Isoptera, Termitidae) are very important constituents of the soil fauna in tropical Africa, being soil or root feeders, or, some of them, active at the soil/wood/litter interface. Soil sampling has shown them to be both abundant and diverse in forest and savanna ecosystems, accounting for a significant part of the live biomass of soil organisms and responsible for a major proportion of soil movement and aeration, contributing also to water penetration (Sands, 1965, Eggleton *et al.*, 1996). Before the current study began, a total of 60 species of soldierless termites belonging to 16 genera had been recorded from the African continent by Sands (1972). A few more genera and species were known from the worker castes alone, but were not described at that time because their characters were not considered to provide as reliable identification as those of the imagos. Since then, further studies of the distinguishing features of the worker castes (Sands, 1992, 1995, 1998) have shown that they can be identified as readily as the imagos, in many cases more easily, and that it is no longer logical to abstain from describing species of soldierless termites recognisable on the basis of their workers alone.

Among the genera previously known, *Amicotermes* was represented by a single species from the southern Congo. The new species described here were, with two exceptions, all collected from rain forest, or degraded derivatives of it, by the members of the termite group at The Natural History Museum, either as part of the NERC-funded TIGER project team in different selected habitats in Cameroon in the Mbamayo forest reserve, or, using a similar transect sampling technique, in the Republic of Congo (Brazzaville) at Mayombe. The purpose of the former project was to examine the effects of different levels of forest degeneration and regeneration, resulting from cultivation and selective logging, on the biodiversity of the soil fauna and its relationship to the carbon cycle (Eggleton *et al.*, 1996).

When the first collections from the Mbalmayo area of Cameroon came to be sorted out, it quickly became evident that the diversity and abundance of termite species in the soil, especially the soil-feeders, of which about half were soldierless Apicotermitinae, was far greater than had been anticipated for this project or had been recorded previously from any ecological sampling, even in rain forests elsewhere. Abundances up to 10,488$m^{-2}$ and live weight biomass up to 123 $gm^{-2}$ were recorded. In a significant proportion of the genera examined, new species were found, and indeed, genera new to science were also present. All of these will have to be described and properly enumerated in due course, but the work presented here covers, as a first instalment, the 11 new species recognised in *Amicotermes,* bringing the total of recorded species for the genus up to 12. This genus was chosen to be examined first because, in an otherwise very difficult group, it has an enteric valve armed with spines and spicules which offer useful taxonomic characters that define species relatively well. Some other genera that remain to be worked out lack this feature and will take much longer to resolve. In the published account of the ecological sampling (Eggleton *et al.* 1996) morphospecies that were thought to be new were designated numerically, there being three such in the genus *Amicotermes*. Further, more careful examination of the material has doubled this number for the Cameroon, and four more were found in the Congo. The last new species was recognised in material acquired earlier from the Upper Guinean Forest in the Ivory Coast. Because of the unevenness of the sampling and knowledge of the ecology of the group in the rest of the Afrotropical zoogeographical region, it is evident that if the entire continent were to be covered in the same detail, the number of species and genera would be multiplied several times over. However, a diligent search through the unidentified accessions from all parts of tropical Africa at The Natural History Museum, including many samples from soil pits collected in the course of earlier ecological studies in Guinean savannah in Nigeria (Sands, 1965a), have failed to produce any further records of *Amicotermes*. It is therefore probably safe to conclude that it is confined to rain forest and this study amounts to a new revision of a single soldierless genus.

## METHODS

In order to speed up the recording of taxonomic data and facilitate its processing by computer, the character set was coded and stored in PANKEY (Pankhurst 1986) DELTA [DEscriptive Language for TAxonomy] (Dallwitz & Paine, 1986, Partridge *et al.*, 1986) format. In this state, it may be converted by several sets of programmes into natural language descriptions, dichotomous printed keys, analysed by cladistic or phenetic procedures, or converted into 'expert systems', that is, interactive computerised polyclaves. Other recently published works (Pankhurst, 1991, Sands, 1992, 1998) go into the details of how this is done. The key and descriptions that follow were produced in this way, as were the comparisons between related species. In order to incorporate the new species into the existing genus, the data from Sands (1972) were coded and added by means of the dedicated editor, DEDIT, to the DELTA file, a copy of which is included as an appendix to illustrate the format, because in the author's view, too few taxonomists are

either aware of its value as a tool, or of its relative simplicity in use once the requirements are understood. The full data matrix itself with ranges, means and standard deviations of measurements has been converted to the key and descriptions and is therefore not repeated here, but it can be supplied on request to those interested as a copy of the entire DELTA file on receipt of a single 3.5 inch high density diskette.

## COMMENTS ON CHARACTERS USED

Some of the characters used require further explanation. Apart from *A. dibogi*, the genus is remarkably homogeneous in its external features, and a great deal of emphasis is therefore placed on the enteric valve armature and on morphometrics. However, it was thought desirable in constructing a key to give summary descriptions of the salient externally observable characters as well as measurements, to supplement the usually distinctive valve structures, because the latter require quite a difficult dissection and slide mount. An annotated character list is given below, followed by a condensed version of the data matrix as used in the HENNIG86 analysis, since it includes *Acholotermes*, the sister genus of *Amicotermes*, as an outgroup.

### *Character descriptions, with states*

Some of the characters require quite difficult dissections to display them properly. Full descriptions of the techniques involved are published elsewhere (Sands 1998), but summary accounts are given below where appropriate.

**Characters 1–5:** The system of coding colour of body parts as an ordered multi-state character has been used since 1965. Only the first five grades (Sands 1965) are required here for the relatively lightly sclerotised worker caste, being re-numbered for each character.

1. Head capsule colour: 1. yellow-white 2. pale yellow 3. yellow 4. pale yellow-brown.
2. Antennal flagellum colour of darkest part 1. yellow-white 2. pale yellow 3. yellow 4. pale yellow-brown.
3. Pronotum colour 1. yellow-white 2. pale yellow 3. yellow.
4. Legs colour 1. yellow-white 2. pale yellow 3. yellow.
5. Abdominal tergites colour 1. hyaline 2. yellow-white 3. pale yellow.

**Characters 6–10:** Head capsule shape is evaluated in facial view. Pilosity is best viewed from below and in front against a lit background; sparse is intended to mean when the setae are spaced further apart than the length of the longest; two lengths of setae are usually evident, the shorter, general pilosity being randomly distributed while the longer, emergent setae are commonly paired on each side of the mid-line. The term 'fontanelle' is used for convenience although workers do not have a true fontanelle, which is the opening of the frontal gland in soldiers and imagos; some species have a pale spot in this position. The degree of inflation of the postclypeus is estimated partly by its dimensions, but also in profile by the regularity of convexity of its outline.

6. Head capsule shape 1. circular 2. short oval near circular 3. oval.
7. Head capsule setae 1. sparse 2. numerous but not dense.
8. Head capsule emergent, longest setae 1. randomly scattered 2. regularly and symmetrically arranged.
9. Fontanelle: 1. present as pale spot or small depression 2. absent.
10. Postclypeus contour: 1. clearly inflated 2. strongly inflated, bulging, length more than half width at ginglymi.

**Characters 11 & 12:** The presence of prominent setae arranged in a line or group on the front surface of the fore coxa may be difficult to detect because in this genus they are not particularly 'spine-like'. If viewed in profile against a lit background they can usually be detected as more robust than normal. Fore tibial apical spurs always number three in this genus with the third, outer spur subject to size variation.

11. Fore coxae 1. without prominent larger setae on anterior surface 2. with one to three prominent larger setae on anterior surface 3. with four or more prominent larger setae arranged in line or group on anterior surface.
12. Fore tibial apical spurs numbering three 1. third well developed, at least half the size of the others 2. third much smaller than the other two.

**Characters 13–17:** Mandible characters including measurements require the cutting edges to be secured transverse, i.e. at right angles, to the optic axis of the lens system containing the graticule. This is particularly important in assessing the visibility and alignment of the left fourth marginal tooth. In order to see these characters clearly, a simple dissection by slitting the adductor apodemes is needed, allowing the mandibles to swing open on their articulations. It is undesirable to detach them from the specimen, since their tetrahedral shape makes them impossible to mount on a slide or secure in a dish in the required position. The dissection is best done with the specimen secured on its back with the finest grade of

stainless steel headless entomological points. The point of a fine scalpel or needle is inserted into the mouth of the specimen, to push aside the labium and hypopharynx. The adductor apodemes are usually visible at the base of the mandibles and can be cut with a single stroke of a fine blade in each direction. A gentle push will then swing the mandibles outwards in turn, and the labrum can be deflected between their separated bases to secure them in position; if necessary the labrum can be pushed out again to allow the mandibles to return to a natural position. The designations of the marginal teeth of the left mandible need further explanation. The first is that immediately proximal to the apical tooth, but the second is incorporated into the cutting edge behind it, forming its curved inner end; the third marginal is separated from the first-plus-second by a distinct notch, while the fourth appears out of alignment with the other marginals, being visible in the gap between the third marginal and the molar prominence; its proximal end, which forms the point of the tooth, is sometimes hidden behind the molar prominence. There are only two marginal teeth on the right mandible in this genus.

13. Left mandible, first marginal tooth 1. with anterior edge distinctly longer than posterior 2. approximately equilateral.
14. Left third marginal tooth with anterior edge 1. shorter than that of first 2. equal in length to that of first 3. longer than that of first.
15. Left fourth marginal tooth in front view 1. with proximal end clear of molar prominence 2. just reaches side of molar prominence 3. with proximal end hidden behind molar prominence.
16. Anterior margin of right first marginal tooth 1. longer than that of second 2. equal in length to that of second 3. shorter than that of second.
17. Right first marginal tooth with exposed posterior edge 1. equal to that of second marginal 2. longer than that of second marginal.

**Characters 18–22:** The configuration of the parts of the alimentary canal as seen through the unopened body wall has been used and illustrated extensively (Sands, 1972, 1995, 1998) in identifying worker castes. The most important features in *Amicotermes* are the position of the enteric valve seating and the length and width of the first section of the proctodeum (P1). The lines of the heart dorsally and the nerve cord ventrally, although sometimes hard to see, are used to mark the positions of features.

18. Junction of mesenteron and proctodeum 1. starting to left of nerve cord in ventral view 2. starting beneath nerve cord in ventral view 3. starting to right of nerve cord in ventral view.
19. Proctodeal first segment 1. shorter, length up to eight times proximal width 2. very long, over eight times proximal width.
20. Proctodeal first segment beyond junction with mesenteron 1. tubular or conical throughout its length 2. dilated to about twice its basal width throughout length.
21. Lateral displacement of enteric valve in unopened abdomen 1. to left of heart in dorsal view 2. to right of heart in dorsal or to left of nerve cord in ventral view.
22. Enteric valve 'seating' third lobe 1. smaller than outer pair 2. approximately equal in size to outer pair.

**Characters 23–45:** The enteric valve is variably sclerotised and armed within its lumen with scales, spines or spicules. In order to display these a dissection is required. Having opened the abdomen by pulling away a section of the body wall with forceps, it is possible simply to pull on the first section of the proctodeum near its distal end to extract the enteric valve from the third (the valve being the second). The valve then needs to be slit longitudinally by inserting into the lumen a micro-scalpel, cleaned, separated where possible from the muscle coats that surround it, and mounted on a microscope slide. The choice of mounting medium is dictated by the fragility of the wisp of tissue that makes up the enteric valve. This prevents the usual dehydration procedures required by most permanent mounts, and necessitates the use of a direct, relaxant temporary medium such as a variant of 'Swan's Berlese'.

Within the enteric valve there are six longitudinal ridges (the 'bourrelets' of Grasse and Noirot (1954)) which carry the main sclerotisations, spines and spicules. The system of numbering the ridges adopted here is that of Sands (1972), in which the single ridge nearest to the front of the specimen, or innermost to the coiling of the gut, is designated 'position number one'; the pair on each side of it are numbered 'position two', the pair beyond them 'position three' and the distal singleton, 'position four'. This is because these positions describe the most common independent dimensions of variation of symmetry, sclerotisation and armature. Because they vary independantly, they have to be described separately for each character and its states. This has resulted in a set of characters that appear repetitive for taxa with hexaradially symmetrical valves; however, to do otherwise would mean losing a large proportion of the information content of this important structure. The characters referring to the positions of the largest spines as proximal, mesal or distal, are not intended to imply that there are no spines on the rest of the ridges, merely that where present, they are smaller than the most elongate and conspicuous spines. The ridges also carry subsidiary

armature of scales, spines or spicules. Between and beyond the ridges the wall of the valve may also bear scales, sometimes armed with small spicules.

**23**. Enteric valve ridges, shape 1. more or less tapering ellipsoid to base of apical spines 2. distinctly 'waisted' at base of apical spines, then wider.
**24**. Enteric valve ridge in position one 1. sclerotised at distal end, pale brown or yellow-brown 2. weakly sclerotised distally, pale yellow or yellow 3. unsclerotised or colourless throughout.
**25, 26, 27**, as **24** but referring respectively to positions two, three and four.
**28**. Main armature of enteric valve ridge in position one 1. without large apical spines (retained to allow for the outgroup, but does not apply to *Amicotermes*) 2. with large backwardly directed erect conical spines 3. with very elongated tapered spines.
**29, 30, 31** as **28** but referring respectively to positions two, three and four.
**32**. Largest apical spines on ridge one 1. numbering 1–9 2. numbering 10–14 3. numbering 15–20 4. numbering over 20.
**33, 34, 35** as **32** but referring respectively to positions two, three and four.
**36**. Longest spines of main armature 1. straight and evenly tapered 2. curved but still evenly tapered.
**37**. Longest apical spines 1. longer than least width of ridges in position three at base of spines 2. shorter than or equal to least width of ridges in position three.
**38**. Subsidiary armature on one or more of enteric valve ridges mainly 1. reticulate 2. with backwardly directed scales 3. with backwardly directed scales fringed with small spines or spicules 4. with small single backwardly directed spines on scales 5. with prominent spines different from or smaller than main armature.
**39**. Subsidiary armature of enteric valve ridges 1. with scales or reticulations well defined, distinct 2. with scales or reticulations indistinct, outlines vague or incomplete.
**40**. Subsidiary armature of one or more of enteric valve ridges 1. prominent, covering entire ridge surface 2. scattered, somewhat sparse 3. very sparse, few scales fringed with spines or spicules.
**41**. Subsidiary armature on one or more enteric valve ridges 1. more or less uniform throughout length of ridge 2. graduated, spines or spicules becoming longer towards distal end of ridge.
**42**. Symmetry of enteric valve armature 1. more or less hexa-radial apart from slight differences in ridge size 2. more or less tri-radial, alternate ridges reduced 3. bilateral due to marked differences in spine and ridge size.
**43**. Membranous wall of enteric valve between and beyond ridges 1. smooth 2. scaly.
**44**. Membranous wall of enteric valve between and beyond ridges 1. armed with minute spines or spicules 2. armed with short spines or spicules.
**45**. Spines or spicules on membranous wall 1. very sparse, scattered 2. numerous but not dense, scattered, fringing scales proximally 3. dense distally, fringing scales proximally.

**Characters 46–60:** Some of the listed ratios may appear unusual in the comparisons they make; they result from selecting measurements that carried large contrasting weighting coefficients in principal component and canonical variates analyses. Such procedures are now so much the routine that no extended treatment is given here. The rationale for the use of complex ratios rather than the actual discriminant functions is explained in Sands (1972) which also lists the set of measurements used as standard in the soldierless termites (and see also Fig. 1). The measurements are given here to three places of decimals because they were recorded automatically from an electronic filar micrometer and processed simultaneously; it seemed less artificial to give them as recorded rather than to round them to fewer places arbritrarily. In practice it has been found that at this level with this equipment measurements are repeatable within about 3%. The measurements used are mostly self explanatory being the maximum distance between identifiable fixed points. Those that need further explanation are the following: Postclypeus width, taken between the inner curves of the ginglymi of the mandibles, which are always recognisable as strongly sclerotised articulations at the corners of the postclypeus; Left mandible, La, distance between the points of the apical and first marginal teeth; L1, distance between the points of the first marginal tooth and the third marginal, because the second is often reduced or obsolete; Lm, distance between the point of the third marginal and the intersection of the fourth, subsidiary marginal (some authers call this the 'molar tooth' but its function is marginal) with the molar prominence, whether this is a notch or the point where the fourth marginal passes behind the prominence; Right mandible, Ra, as left; R1, distance between the points of the first and second marginal teeth; Rm, distance between point of second marginal and the intersection of its hind margin with the molar plate; the front edge of this tooth is also measured, in order to provide a 'second marginal index' to indicate its degree of reduction. It is important when taking measurements to ensure that the specimen is held exactly transverse to the optic axis of the lens tube of the eyepiece containing the graticule.

**46**. Head capsule width (range, mean, SD) mm.
**47**. Postclypeus width (range, mean, SD) mm.
**48**. Postclypeus length (range, mean, SD) mm.
**49**. Left mandible index (range, mean).

50. Right mandible index (range, mean).
51. Right second marginal index (range, mean).
52. Right first to second marginal index (range, mean).
53. Pronotum width (range, mean, SD) mm.
54. Pronotum length (range, mean, SD) mm.
55. Hind tibia length (range, mean, SD) mm.
56. Fore tibia length (range, mean, SD) mm.
57. Fore tibia thickness (range, mean, SD) mm.
58. Fore tibial index (length over width) (range, mean).
59. Left mandible, complex ratio La divided by L1.Lm (range, mean).
60. Right mandible, complex ratio Ra divided by R1.Rm (range, mean).

### Condensed data matrix with outgroup

The condensed data matrix, outgroup included, is shown in Table 1. The programmes used to process descriptions and keys were DESCRIP3 and KCONP with KCONI, the interactive key construction programme and KPRINT from the PANKEY set (Pankhurst, 1986, 1991). An MS-DOS binary file of the data to run with PANKEY ONLIN7 that will provide an interactive but un-illustrated polyclave is available, for use in conjunction with the illustrations in this paper, from the author on request and provision of one MS-DOS-formatted 3.5" or 5.25" HD diskette. The programme itself must be obtained from EXETER SOFTWARE, 100 North Country Road, Setauket, New York 11733, USA. The advantage of a polyclave is that it can be entered with any character found easiest by the user and any path can be followed through the data matrix, as opposed to the fixed path set by a dichotomous key.

The Cameroon material examined was all collected by members of the TIGER team, some in the period July to December, 1992 and some later, up to 1997. They were variously Drs D. Bignell, P. Eggleton, D. Jones, J. Lawton and T. Wood, and Luc Dibog (Eggleton *et al.*, 1996). The Congo material was collected later, in the course of a single expedition by Dr Eggleton and Mr.Davies. It is not practicable to distinguish the contributions of individual participants in the lists of material examined.

## *AMICOTERMES* Sands 1972

(Amicus, L., 'friend (ly), kind')

Type-species: ***Amicotermes galenus*** Sands 1972

*Imago.* See Sands 1972. None known apart from Type-species.

*Worker.* Small to medium-sized, head capsule width 0.565 to 0.800 mm; head capsule setae usually sparse; postclypeus strongly inflated, bulging, length more than half its width at the ginglymi, width 0.3–0.434, length 0.154–0.25 mm. Fore tibia moderately to strongly swollen, index (length/width) 2.954 to 4.759. Apical teeth of mandibles longer than first marginals, left mandible index 0.697 to 1.205, right mandible index 0.879 to 1.374; left fourth marginal tooth with proximal point clear or hidden behind molar prominence, complex ratio La divided by L1.Lm 17.556 to 37.866; point of first marginal tooth of right mandible behind line from apical to second marginal, front edge of first marginal shorter than or subequal to that of second, its exposed posterior edge longer than that of the second marginal, right first to second marginal index 1.35 to 2.094; second marginal prominent, second marginal index 0.788 to 1.262, complex ratio Ra divided by R1.Rm 20.164 to 34.01. Crop large with hemispherical 'bursters' on front dorsum, gizzard bell-shaped, not tapered to enter mesenteron. Mesenteric junction with proctodeum nearly transverse, slightly angled, in ventral view of unopened abdomen beneath or to right of malpighian knot, beneath or slightly to left or right of nerve cord. Enteric valve seating three-lobed, the third, inner, smaller than or equal to the outer two, connected to third section of proctodeum ('pouch') by very long neck, left lateral or dorsal in position in unopened abdomen. Main armature of enteric valve ridges consists of tapered apical spines, protruding through valve exit into third section of proctodeum, subsidiary armature varies from prominent spines different from or smaller than main armature to scales fringed with minute spicules or bearing single small spines; membranous wall of enteric valve between and beyond ridges usually scaly, with spicules.

*Amicotermes* is a genus easily recognised in the worker caste by the several features of the abdominal anatomy visible from the exterior and especially by the very characteristic internal armature of the enteric valve, which also supplies many important specific characters. The workers are small to medium-sized among soldierless Apicotermitinae, and although fairly common, are not the most numerous members of this group to be found in ecological soil samples.

Autothysis (the suicidal rupture of the body wall by the contraction of abdominal muscles, accompanied by the discharge of defensive fluids or gut contents) as a defence mechanism aginst small predators such as ants is common in the soldierless Apicotermitinae (Sands, 1972, 1982) and its development may be responsible for the loss of the soldier caste. In this genus, extreme autothysis is characterised by a pair of hemi-spherical 'bursters', apparently inflated from the front of the crop by pressure from the contracting abdominal wall muscles, which cause the dorsal body wall to rupture in front of the first abdominal tergite, so that few specimens in any series are not so damaged and most of these have distorted abdomens. . Only in one species, *A. tithasus* Sands, 1972 of the sister-group *Acholotermes* has a similar bell-shaped proventriculus been observed and here the rupture of

**Table 1** Condensed data matrix, outgroup (in parentheses) included. Continuous variables (measurements) are coded as means allocated to key states, while variable multi-states are coded as medians. Missing or inapplicable data is shown as a query.

| | characters 1–60 | | | | | |
|---|---|---|---|---|---|---|
| (Acholotermes) | 2322121122 | 1111132211 | 2213333111 | 1??????211 | 112125??34 | ???????6?? |
| autothysius | 2311122122 | 2111122211 | 2121111333 | 3213212512 | 2221321222 | 3412211322 |
| camerunensis | 1111121222 | 2121222222 | 2112222222 | 2323212521 | 2121242223 | 3422333312 |
| congoensis | 1211121212 | 3212132211 | 2222222333 | 3212122512 | 2221242234 | 3322221422 |
| cristatus | 2211121212 | 3222232211 | 2211111222 | 2111112212 | 1122343333 | 33?3331422 |
| dibogi | 2312121122 | 2121232122 | 1213333333 | 3222212511 | 2121132323 | 3322331512 |
| galenus | 3311211122 | 3211122211 | 2122222333 | 3112111512 | 2321264456 | 3434321524 |
| gasteruptus | 1311121122 | 2111132211 | 2121111333 | 3313121522 | 2221221222 | 331?111322 |
| ivorensis | 2222221112 | 1221122211 | 2212222333 | 3111111323 | 22111???33 | 3423221312 |
| mayombei | 1111121222 | 3112232211 | 2121111333 | 3113122512 | 2322332234 | 4311221412 |
| multispinus | 1111121222 | 3122232211 | 2122222333 | 3314121522 | 22222?2223 | 32?1111322 |
| mbalmayoensis | 1311122222 | 1121332211 | 2112222333 | 3212212422 | 1121364334 | 344344?422 |
| spiculatus | 2211131222 | 3122132211 | 2113212222 | 2113112521 | 2322243323 | 3423432412 |

the body wall in autothysis appears to be mediated more by pressure from the crop against the underside of the slightly inflated colon which crosses it at this point. The proctodeal first segment beyond the junction with the mesenteron is usually tubular throughout its length. The mandibles are generally similar to those of *Acholotermes*.

In *Acholotermes* the main armature of the hexaradially symmetrical enteric valve ridges is never more than a few minute spicules fringing scales, but the membranous wall between and beyond the ridges is scaly and spiculate like that of *Amicotermes*.The other genera having enteric valve armature apparently related to that of *Amicotermes* are *Apagotermes* and *Ateuchotermes*. The former is smaller and the latter larger, both having different mandibles from *Amicotermes* and both having specialised features of their valve armature, which, however, do not include a spiculate and scaly or carunculate inter-ridge membrane (Sands 1972, 1998).

## Key to the species of *AMICOTERMES* Sands 1972

The disadvantages of dichotomous keys resulting from forcing on the user a single path chosen by the author through the data matrix are well-known. In the key which follows, some couplets appear longer than usual, especially when nearing an identification. This is necessitated by the extreme difficulty of identifying worker castes on the basis of variable characters and some that require delicate dissections. The solution offered is a combination of more easily observed features that are currently diagnostic and may provide a simple identification but might break down because the variation is imperfectly known, and more difficult but possibly more reliable characters. This is an attempt at compromise between the fallible simplicity of a normal dichotomous key and the greater flexibility of a polyclave.

1 Head capsule width 0.763 to 0.800 mm, postclypeus width 0.413 to 0.434 mm ..... 2

– Head capsule width 0.565 to 0.717 mm, postclypeus width 0.300 to 0.395 mm ..... 3

2 Hind tibia length 0.725 mm, fore tibia length 0.563 mm, fore tibia thickness 0.13 mm, fore tibial index (length over width) 4.327, left mandible index 1.092, right mandible, complex ratio Ra divided by R1.Rm, 31.28. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two. Left mandible, first marginal tooth with anterior edge distinctly longer than posterior, left fourth marginal tooth in front view with proximal end clear of molar prominence; anterior margin of right first marginal tooth equal in length to that of second. Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, longest apical spines on ridge one numbering 1–9, those of ridges in position three longer than least width at base of spines, subsidiary armature on one or more of enteric valve ridges mainly with prominent spines different from or smaller than main armature, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined, distinct, symmetry of enteric valve armature bilateral due

to marked differences in spine and ridge size, spines or spicules on membranous wall numerous but not dense, scattered, fringing scales proximally ..... ..... ***galenus*** (page 159, Figs 76–82, 177, 178)

– Hind tibia length 0.779 to 0.82 mm, fore tibia length 0.614 to 0.677 mm, fore tibia thickness 0.159 to 0.173 mm, fore tibial index (length over width) 3.602 to 4.077, left mandible index 0.896 to 0.978, right mandible, complex ratio Ra divided by R1.Rm, 20.164 to 26.881. Fore coxae without prominent larger setae on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Left mandible, first marginal tooth approximately equilateral, left fourth marginal tooth in front view just reaches side of molar prominence, or with proximal end hidden behind molar prominence; anterior margin of right first marginal tooth shorter than that of second, enteric valve ridges, more or less tapering ellipsoid to base of apical spines, longest apical spines on ridge one numbering 10–14, those of ridges in position three shorter than or equal to least width, subsidiary armature on one or more of enteric valve ridges mainly with small single backwardly directed spines on scales, more or less uniform throughout length of ridge, scales or reticulations indistinct, outlines vague or incomplete, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size, spines or spicules on membranous wall dense distally, fringing scales proximally ..... ... ***mbalmayoensis*** (page 163, Figs 125–137, 183, 184)

3 Symmetry of enteric valve armature more or less hexaradial apart from slight differences in ridge size ..... 4

– Symmetry of enteric valve armature more or less triradial, alternate ridges reduced, or bilateral due to marked differences in spine and ridge size ..... 6

4 Lateral displacement of enteric valve in unopened abdomen to left of heart in dorsal view, first section of proctodeum very long. Main armature of enteric valve ridges with very elongated tapered spines, ridges unsclerotised or colourless, spines or spicules on membranous wall very sparse, scattered ..... ..... ***dibogi*** (page 158, Figs 62–75, 176)

– Lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view. Main armature of enteric valve ridges with large backwardly directed erect conical spines, ridges sclerotised at distal ends, pale yellow to pale brown or yellow-brown, spines or spicules on membranous wall numerous or dense distally, fringing scales proximally ..... 5

5 Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third much smaller than the other two. Left mandible, third marginal tooth with anterior edge equal in length to that of first. Proctodeal first segment shorter, up to eight times proximal width, enteric valve 'seating' third lobe approximately equal in size to outer pair. Enteric valve ridges sclerotised at distal end, pale brown or yellow-brown, largest spines on ridges numbering up to 12; subsidiary armature on one or more ridges mainly with backwardly directed, well defined distinct scales, some fringed with small, scattered, sparse spines or spicules, more or less uniformly distributed throughout length of ridge; membranous wall of enteric valve between and beyond ridges armed with short spines or spicules, dense distally, fringing scales proximally ..... ..... ***cristatus*** (page157, Figs 47–61, 173, 174)

– Fore coxae without prominent larger setae on anterior surface, or with one to three at most, fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Left mandible, third marginal tooth with anterior edge shorter than that of first. Proctodeal first segment longer, over eight times proximal width, enteric valve 'seating' third lobe smaller than outer pair. Enteric valve ridges weakly sclerotised distally, pale yellow or yellow, largest spines on ridges numbering 12–25; subsidiary armature on one or more ridges mainly with prominent spines different from or smaller than main armature, borne on indistinct scales or reticulations, covering entire ridge surface, graduated, spines or spicules becoming longer towards distal ends of ridges; membranous wall of enteric valve between and beyond ridges armed with minute spines or spicules, numerous but not dense, scattered, fringing scales proximally ..... ..... ***camerunensis*** (page 154, Figs 16–28, 175)

6 Hind tibia length 0.784 to 0.794 mm, fore tibia length 0.620 to 0.625 mm Enteric valve main armature of all ridges with large backwardly directed erect conical spines, but ridge in position one unsclerotised or colourless throughout, ridge two weakly and ridges three and four fully sclerotised yellow-brown; subsidiary armature of enteric valve ridges prominent, covering entire ridge surface ..... ***spiculatus*** (page 165, Figs 151–161, 186)

– Hind tibia length 0.565 to 0.736 mm, fore tibia length 0.489 to 0.574 mm Enteric valve main armature of all ridges with very elongated tapered spines, uniformly sclerotised, yellow-brown or weakly sclerotised distally, pale yellow or yellow; subsidiary armature of enteric valve ridges scattered, somewhat or very sparse, few scales fringed with spines or spicules ..... 7

7 Longest apical spines of enteric valve armature shorter than or equal to least width of ridges in position three, subsidiary armature of enteric valve ridges with scales or reticulations well defined, distinct ..... 8

– Longest apical spines of enteric valve armature longer than least width of ridges in position three at base of spines, subsidiary armature of enteric valve ridges with scales or reticulations indistinct, outlines vague or incomplete ..... 10

8 Left fourth marginal tooth in front view just reaches side of molar prominence. Symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size, membranous wall of enteric valve between and beyond ridges armed with short spicules ..... ..... ***mayombei*** (page 162, Figs 111–124, 181, 182)

– Left fourth marginal tooth in front view with proximal end clear of molar prominence. Symmetry of enteric

valve armature more or less tri-radial, alternate ridges reduced, membranous wall of enteric valve between and beyond ridges armed with minute spicules ..... 9

9 Head capsule with emergent, longest setae regularly and symmetrically arranged. Fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two. Enteric valve 'seating', third lobe approximately equal in size to outer pair; enteric valve ridges weakly sclerotised distally, pale yellow or yellow; spines or spicules on membranous wall of valve between ridges numerous but not dense, scattered, fringing scales proximally ..... ***congoensis*** (page156, figs 29–46, 171, 172)

– Head capsule with emergent, longest setae randomly scattered. Fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Enteric valve 'seating', third lobe smaller than outer pair, enteric valve ridges sclerotised at distal ends, pale brown or yellow-brown, spines or spicules on membranous wall dense distally, fringing scales proximally ..... ***autothysius*** (page 153, figs 1–15, 169, 170)

10 Anterior margin of first marginal tooth of right mandible equal in length to that of second. Enteric valve 'seating' third lobe approximately equal in size to outer pair; largest apical spines of enteric valve armature on ridges one and three numbering 1–9; subsidiary armature on enteric valve ridges very sparse, with a few backwardly directed scales fringed with small spines or spicules, or with small single backwardly directed spines on scales; membranous wall of enteric valve between and beyond ridges smooth, with very sparse, scattered spines or spicules ..... ***ivorensis*** (page 161, figs 99–110, 180)

– Anterior margin of right first marginal tooth shorter than that of second. Enteric valve 'seating' third lobe smaller than outer pair; largest apical spines of enteric valve armature on ridge one numbering 10–20, those on ridges three numbering 10 to over 20; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature; membranous wall of enteric valve between and beyond ridges scaly, with numerous but not dense scattered spicules, fringing scales proximally ..... 11

11 Head capsule with emergent, longest setae regularly and symmetrically arranged. Left mandible, third marginal tooth with anterior edge equal in length to that of first. Enteric valve ridges weakly sclerotised distally, pale yellow or yellow, positions one and three with 20 or more apical spines; membranous wall of enteric valve between and beyond ridges armed with short spicules ..... ***multispinus*** (page 164, figs 138–150, 185)

– Head capsule with emergent, longest setae randomly scattered. Left mandible, third marginal tooth with anterior edge shorter than that of first. Enteric valve ridges sclerotised at distal end, pale brown or yellow-brown, positions one and three with 10–20 apical spines; membranous wall of enteric valve between and beyond ridges armed with minute spicules ..... ***gasteruptus*** (page 160, figs 83–98, 179)

## DESCRIPTIONS OF SPECIES

### *Amicotermes autothysius* sp. n.

(Figs 1–15, 169, 170)

Head capsule pale yellow or yellow, antennal flagellum colour of darkest part yellow or pale yellow-brown, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae numerous but not dense, emergent, longest setae randomly scattered. Fontanelle absent. Fore coxae without prominent larger setae or with up to four or sometimes more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior or approximately equilateral, third marginal tooth with anterior edge shorter than or equal in length to that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth equal in length to or shorter than that of second.

Junction of mesenteron and proctodeum starting beneath or to right of nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, all ridges sclerotised at distal end, pale brown or yellow-brown, main armature with very elongated tapered spines, the largest on ridges one and four numbering 1–14, those on ridges two, 1–9, and on ridges three, 10–20, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; longest spines of main armature straight or curved but still evenly tapered, shorter than or equal to least width of ridges in position three; subsidiary armature on one or more of enteric valve ridges mainly with scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly, armed with minute spicules, dense distally, fringing scales proximally.

*Measurements and diagnostic ratios* [24 individuals from 9 series]:

Head capsule width 0.565 to 0.717 mm (mean 0.633 SD 0.039).

Postclypeus width 0.300 to 0.395 mm (mean 0.332 SD 0.026).
Postclypeus length 0.154 to 0.233 mm (mean 0.185 SD 0.021).
Left mandible index 0.697 to 1.144 (mean 0.843).
Right mandible index 0.879 to 1.278 (mean 1.040).
Right second marginal index 0.817 to 1.166 (mean 0.982).
Right first to second marginal index 1.432 to 2.095 (mean 1.734).
Pronotum width 0.375 to 0.495 mm (mean 0.424 SD 0.027).
Pronotum length 0.169 to 0.293 mm (mean 0.209 SD 0.024).
Hind tibia length 0.565 to 0.706 mm (mean 0.649 SD 0.032).
Fore tibia length 0.489 to 0.556 mm (mean 0.517 SD 0.018).
Fore tibia thickness 0.131 to 0.144 mm (mean 0.138 SD 0.004).
Fore tibial index (length over width) 3.441 to 3.984 (mean 3.741).
Left mandible, complex ratio La divided by L1.Lm 17.556 to 29.807 (mean 23.846).
Right mandible, complex ratio Ra divided by R1.Rm 20.717 to 34.01 (mean 25.475).

COMPARISONS. The Cameroonian species most closely related to *A. autothysius* is *A. gasteruptus*, from which it is only distinguished by the shorter apical spines of the enteric valve main armature and the more distinct outlines of the scales of the subsidiary armature. Its symmetry in *A. autothysius* also tends towards the bilateral rather than being clearly triradial. This pair of species forms a terminal group in all the trees apart from the Saitou and Nei (1987) Neighbour-Joining tree. *A. camerunensis* has the fourth marginal tooth of the left mandible just reaching the side of the molar prominence, a proportionately longer fore tibia, and a hexa-radial enteric valve armature with large straight conical spines. In *A. congoensis* the third fore tibial apical spur is reduced, being one third or less the length of the others, and the third lobe of the enteric valve seating is roughly equal in size to the outer pair; the largest apical spines of the enteric valve armature are generally longer and the ridges more clearly triradial. *A. cristatus* is generally larger and also shares the features that separate *A. camerunensis*. *A. dibogi* differs in the proportions of the mandibular teeth, but most notably in the greater length and inflation of the first proctodeal segment, hence also the dorsal position of the enteric valve seating; the valve armature is quite different from any other member of the genus being armed with very fine long apical spines and hightly spiculate fringed scales. *A. galenus* is, again, larger and the enteric valve armature differs in the length and straightness of the apical spines. *A. ivorensis* has fewer head setae and lacks prominent fore coxal setae, while its enteric valve has fewer but longer apical spines and a much less developed subsidiary armature. In *A. mayombei* the fourth marginal tooth of the left mandible just reaches the side of the molar prominence; the spiculate fringes of the inter-ridge membrane of the enteric valve are denser and longer than in *A. autothysius* and the symmetry of the valve is more bilateral. *A. mbalmayoensis* is considerably larger and its enteric valve is hexa-radially symmetrical with differently shaped ridges on which the subsidiary armature consists of single small spines on indistinct scales, more or less uniform over the entire ridge surface. In *A. multispinus* the left fourth marginal tooth just reaches the side of the molar prominence; the enteric valve ridges carry longer and more numerous apical spines, while the scales of the subsidiary armature are very indistinct in outline. Finally, *A. spiculatus* has longer and slightly more slender legs, and the enteric valve is bilaterally symmetrical, ridges three and four being differentially sclerotised and three, much larger while ridge one is colourless and two intermediate; the entire ridge surfaces are spiny with the subtending scales very weakly marked.

MATERIAL EXAMINED. [total 13 series]
Holotype, worker and Paratypes from Type series (field collection number, $H_2P$-2), **Cameroon**: Mbalmayo Forest Reserve, Ekombitie July 1996 (*Eggleton et al.*); other Paratype material, Eboufek, July–Aug.1992, Ekombitie, Ebogo, Nov. 1995, Ebogo, Ekombitie, 5 series, Feb. 1996, Ebogo, Mar. 1996, Ekombitie, Ebogo, 3 series, July 1996, (*Eggleton et al.*) (all in BMNH).

## *Amicotermes camerunensis* sp. n.

(Figs 16–28, 175)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule circular or short oval near circular, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae without or with one to three prominent larger setae on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior edge of first marginal tooth equal in length to or shorter than that of second.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view, proctodeal

first segment longer, over eight times proximal width, tubular throughout its length or dilated to about twice its basal width, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view; enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, weakly sclerotised distally, pale yellow or yellow, main armature of all valve ridges with large backwardly directed erect conical spines, the largest numbering 10–20, the longest straight and evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; subsidiary armature on one or more of enteric valve ridges mainly with prominent spines different from or smaller than main armature covering entire ridge surface, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations indistinct, their outlines vague or incomplete; membranous wall of enteric valve between and beyond ridges scaly, armed with numerous but not dense minute spines or spicules, scattered, fringing scales proximally.

*Measurements and diagnostic ratios* [15 individuals from 5 series]:

Head capsule width 0.652 to 0.711 mm (mean 0.687 SD 0.016).
Postclypeus width 0.340 to 0.370 mm (mean 0.360 SD 0.009).
Postclypeus length 0.172 to 0.215 mm (mean 0.199 SD 0.012).
Left mandible index 0.731 to 0.902 (mean 0.839).
Right mandible index 0.992 to 1.187 (mean 1.093).
Right second marginal index 0.806 to 1.175 (mean 0.973).
Right first to second marginal index 1.643 to 2.088 (mean 1.820).
Pronotum width 0.411 to 0.468 mm (mean 0.447 SD 0.017).
Pronotum length 0.192 to 0.251 mm (mean 0.218 SD 0.019).
Hind tibia length 0.696 to 0.794 mm (mean 0.74 SD 0.026).
Fore tibia length 0.589 to 0.632 mm (mean 0.607 SD 0.014).
Fore tibia thickness 0.147 to 0.205 mm (mean 0.168 SD 0.013).
Fore tibial index (length over width) 2.954 to 4.121(mean 3.624).
Left mandible, complex ratio La divided by L1.Lm 18.546 to 23.477 (mean 21.018).
Right mandible, complex ratio Ra divided by R1.Rm 22.193 to 29.197 (mean 25.539).

COMPARISONS. *A. camerunensis* has already been compared with *A. autothysius* under that species. *A. congoensis* differs in having shorter legs; the anterior edge of the left third marginal tooth is equal to that of the first and the fourth marginal has its proximal end clear of the side of the molar prominence; the third lobe of the enteric valve seating is approximately equal to the other two, while the spines of the main armature are curved on a tri-radial valve. In *A. cristatus* the third fore tibial apical spur is smaller and the front edge of the third marginal tooth of the left mandible is equal in length to that of the first; the apical spines of the main enteric valve armature are fewer and the subsidiary armature is much less developed. *A. dibogi* is characterised externally by the very long, dilated P1 which pushes the enteric valve seating with its three equal lobes into a dorsal position to the left of the heart line; the main armature of the enteric valve is quite different, with its slender apical spines and the subsidiary armature with well defined scales fringed with spicules. *A. galenus* is larger and has the front edge of the left first marginal tooth longer than the hind edge, with the fourth marginal clear of the molar prominence; the mandibular indices are higher; the apical spines of the main enteric valve armature are fewer, more slender and longer on a bilaterally symmetrical valve. *A. gasteruptus* is smaller, with shorter hind tibiae; its enteric valve ridges are 'waisted' apically with elongated tapered curved spines, fewer in number on ridges two and four of a tri-radially symmetrical valve. While about the same size, *A. ivorensis* has shorter legs and the left fourth marginal tooth clear of the molar prominence; the third lobe of the enteric valve seating is approximately equal to the other two and the main armature has fewer, longer apical spines on a tri-radial valve with reduced subsidiary armature. In *A. mayombei* the front edge of the left first marginal tooth is longer than its hind edge and equal to that of the third, while the front edge of the right first marginal is shorter than that of the second; the enteric valve ridges are, again, 'waisted' and one, two and four bear fewer spines on a bilaterally symmetrical valve. *A. mbalmayoensis* is larger and the subsidiary armature of its enteric valve ridges consists of small single spines on scales, more or less uniform throughout the length of each ridge. *A. multispinus* is smaller, with shorter legs; the front edges of the left first and third marginals are subequal and that of the right first marginal is shorter than that of the second; the enteric valve ridges are again, 'waisted' and the longest apical spines on ridges three are longer than the least width of these ridges, the symmetry of the valve being tri-radial. Finally, in *A. spiculatus* the front edges of the left first and third marginals are subequal, the proximal end of the fourth marginal is clear of the molar prominence and the front edge of the right first marginal is shorter than that of the second; the enteric

valve armature, while superficially similar, is distinctive in being bilaterally symmetrical owing to differential sclerotisation of the ridges.

MATERIAL EXAMINED. [total, 6 series]
Holotype worker and Paratypes from Type series (field collection no. Soil#1), **Cameroon**: Mbalmayo Forest Reserve, Eboufek July–Aug. 1992 (*Eggleton et al.*); other Paratype material, Ebogo, 2 series, July–Aug. 1992, Ebogo, Feb. 1996, Ekombitie, Ebogo July 1996 (*Eggleton et al.*) (all in BMNH).

## *Amicotermes congoensis* sp. n.

(Figs 29–46, 171, 172)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, pale yellow or yellow, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae sparse or numerous but not dense, emergent, longest setae regularly and symmetrically arranged. Fontanelle present as pale spot or small depression or absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior or approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubularl throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines or distinctly 'waisted' at base of apical spines, then wider, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on ridges one and three numbering 10–14, those on ridges two and four numbering up to 10, longest spines curved but still evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse, prominent spines different from or smaller than main armature, graduated, spines becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly armed with minute numerous but not dense spicules, scattered, fringing scales proximally.

*Measurements and diagnostic ratios* [15 individuals from 4 series]

Head capsule width 0.659 to 0.705 mm (mean 0.684 SD 0.014).
Postclypeus width 0.340 to 0.380 mm (mean 0.365 SD 0.013).
Postclypeus length 0.177 to 0.215 mm (mean 0.197 SD 0.011).
Left mandible index 0.808 to 1.205 (mean 0.940).
Right mandible index 0.971 to 1.374 (mean 1.168).
Right second marginal index 0.885 to 1.174 (mean 1.019).
Right first to second marginal index 1.350 to 1.921 (mean 1.695).
Pronotum width 0.410 to 0.472 mm (mean 0.450 SD 0.019).
Pronotum length 0.184 to 0.236 mm (mean 0.213 SD 0.017).
Hind tibia length 0.670 to 0.710 mm (mean 0.692 SD 0.013).
Fore tibia length) 0.535 to 0.574 mm (mean 0.553 SD 0.011).
Fore tibia thickness 0.136 to 0.150 mm (mean 0.142 SD 0.004).
Fore tibial index (length over width) 3.598 to 4.185 (mean 3.889).
Left mandible, complex ratio La divided by L1.Lm 17.791 to 37.866 (mean 25.316).
Right mandible, complex ratio Ra divided by R1.Rm 21.345 to 32.805 (mean 25.805).

COMPARISONS. *A. congoensis* has already been compared with the preceding two species; It forms a terminal pair with *A. multispinus* in most of the phenetic trees, but joins with *A. autothysius, A. gasteruptus* and *A. mayombei* at node 16 in the strict consensus tree; the comparisons with the two latter species are given below. *A. cristatus* is larger with longer fore legs and the left fourth marginal tooth just reaching the side of the molar prominence; the spines of the main armature of the enteric valve ridges are large, straight and conical on a more or less hexa-radially symmetrical valve. *A. dibogi* has the front edge of the left third marginal tooth shorter than that of the first, and the fourth just reaching the side of the molar prominence; the main distinguishing feature is again the long dilated P1 with the enteric valve seating dorsal, to the left of the heart; the hexa-radial enteric valve armature with its fine straight spines and spiculate scales is unique in the genus. *A. ivorensis* lacks prominent setae on the fore coxa, the front edge of the left third

marginal tooth is shorter than that of the first, and of the right first marginal, equal to that of the second; the longest apical spines of the main enteric valve armature are longer than the least width of ridges three but all armature, main and subsidiary, is notably sparse. *A. galenus* is larger, the front edge of the left third marginal is shorter than that of the first and that of the right first marginal equal to the second; the longest apical spines of the main enteric valve armature are straight, longer than the least width of ridges three and fewer on the bilaterally symmetrical valve. *A. gasteruptus* is slightly smaller, the front edge of the left third marginal tooth is shorter than the first and the third lobe of the enteric valve seating is smaller than the other two; the longest apical spines of the main enteric valve armature are longer than the least width of ridges three and the scales of the subsidiary armature are indistinct. *A. mayombei* has the third fore tibial apical spur well developed, the fourth marginal tooth of the left mandible just reaching the side of the molar prominence, and the third lobe of the enteric valve seating smaller than the outer pair; the enteric valve armature is bilaterally symmetrical. *A. mbalmayoensis* is considerably larger; it lacks prominent setae on the fore coxae and the third apical spur of the fore tibia is well developed; the proximal end of the fourth marginal tooth of the left mandible reaches the side of the molar prominence or is hidden behind it; the third lobe of the enteric valve seating is smaller than the outer pair and the longest apical spines of the main enteric valve armature are straight on a hexa-radially symmetrical valve. *A. multispinus* is slightly smaller and has the third fore tibial spur well developed; the left fourth marginal reaches the side of the molar prominence; the longest apical spines of the enteric valve armature are longer than the least width of ridges three and more numerous on one and three. Finally, *A. spiculatus* is about the same size but has markedly longer legs, the fore tibiae with well developed third spurs; the apical spines of the main armature of the enteric valve are straight and conical and the symmetry is bilateral largely because of markedly different degrees of sclerotisation of the ridges.

MATERIAL EXAMINED. [total 5 series]
Holotype worker and Paratypes from Type series (field collection no. $T_1$.13), **Congo (Brazzaville)**: Mayombe, Feb. 1997; other Paratype material, Feb. 1997, 4 series (*Eggleton* and *Davies*) (all in BMNH).

## *Amicotermes cristatus* sp. n.

(Figs 47–61, 173, 174)

Head capsule pale yellow, antennal flagellum, colour of darkest part, pale yellow or yellow, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular or oval, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle present as pale spot or small depression or absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior margin of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, sclerotised at distal ends, pale brown or yellow-brown, main armature of all ridges with large backwardly directed erect conical spines, those on ridges one, three and four numbering up to14, those on ridges two, less than 10, straight and evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; subsidiary armature of enteric valve ridges with scattered, sparse spines or spicules on scales, scales or reticulations well defined, distinct, more or less uniform throughout length of ridge; membranous wall of enteric valve between and beyond ridges scaly, armed with short spicules, dense distally, fringing scales proximally.

*Measurements and diagnostic ratios* [8 individuals from 3 series]:

Head capsule width 0.673 to 0.717 mm (mean 0.690 SD 0.015).
Postclypeus width 0.360 to 0.395 mm (mean 0.379 SD 0.013).
Postclypeus length 0.187 to 0.228 mm (mean 0.204 SD 0.015).
Left mandible index 0.871 to 0.965 (mean 0.915).
Right mandible index 0.968 to 1.265 (mean 1.099).
Right second marginal index 0.861 to 1.113 (mean 0.963).
Right first to second marginal index 1.523 to 1.816 (mean 1.701).
Pronotum width 0.448 to 0.512 mm (mean 0.479 SD 0.021).
Pronotum length 0.221 to 0.265 mm (mean 0.241 SD 0.016).

Hind tibia length 0.727 to 0.765 mm (mean 0.742 SD 0.015).

Fore tibia length 0.575 to 0.608 mm (mean 0.589 SD 0.011).

Fore tibia thickness 0.144 to 0.148 mm (mean 0.146 SD 0.002).

Fore tibial index (length over width) 3.974 to 4.165 (mean 4.049).

Left mandible, complex ratio La divided by L1.Lm 21.913 to 26.987 (mean 24.192).

Right mandible, complex ratio Ra divided by R1.Rm 21.978 to 27.22 (mean 24.533).

COMPARISONS. *A. cristatus* is one of the more distinctive species with its 'crest' of large conical spines on the enteric valve ridges and has already been compared with the three that precede it. The next species, *A. dibogi*, is distinctive in the longer, dilated P1 that pushes the enteric valve seating around to the dorsal side of the unopened abdomen; the fine apical spines of the enteric valve main armature and the highly spiculate fringed scales of the subsidiary armature are also different from any other species. *A. galenus* is larger with higher mandibular indices and has the front edge of the left first marginal tooth longer than the hind edge, the third marginal shorter than the first, while the fourth marginal is clear of the molar prominence; the front edge of the right first marginal is equal to that of the second; the ridges of the enteric valve armature are 'waisted' at the base of the apical spines, which are elongated, straight and longer than the least width of ridges three, the symmetry of the valve being bilateral. *A. gasteruptus* is considerably smaller and has the third lobe of the enteric valve armature smaller than the outer pair; the valve ridges are 'waisted' at the base of the apical spines which are elongated, curved, and longer than the least width of ridges three, the symmetry of the valve being tri-radial. *A. ivorensis* is smaller, lacks prominent setae on the fore coxae, has the left third marginal tooth shorter than the first and the fourth marginal clear of the molar prominence; the front edge of the right first marginal tooth is equal to that of the second; the apical spines of the main armature of the enteric valve ridges are straight but elongated and tapered, longer than the least width of ridges three, on a tri-radially symmetrical valve with subsidiary armature and that between the ridges very sparse. *A. mayombei* has well developed third fore tibial spurs, the third lobe of the enteric valve seating smaller than the outer pair and the left third marginal tooth shorter than the first; the ridges of the enteric valve armature are 'waisted' at the base of the apical spines, which are elongated and more numerous on ridges three on a bilaterally symmetrical valve. *A. mbalmayoensis* is considerably larger without prominent setae on the fore coxae and with well developed third fore tibial spurs; the third lobe of the enteric valve seating is smaller than the outer pair; the apical spines of the main armature of the enteric valve ridges are straight but elongated and tapered, while the subsidiary armature consists mainly of small single spines on scales. *A. multispinus* is smaller, with well developed third fore tibial spurs and the third lobe of the enteric valve seating is smaller than the outer pair; the valve ridges are 'waisted' at the base of the apical spines which are elongated, curved, more numerous and longer than the least width of ridges three, the symmetry of the valve being tri-radial. Lastly, *A. spiculatus* also has well developed third fore tibial spurs, while the left fourth marginal tooth is clear of the molar prominence; the enteric valve armature is distinctive in being bilateral owing to differential sclerotisation of the ridges, one being colourless and three fully sclerotised.

MATERIAL EXAMINED. [total 3 series]
Holotype worker and Paratypes from Type series (field collection no. $T_2$.11), **Congo (Brazzaville)**: Mayombe, Feb. 1997; other Paratype material, Feb. 1997, 2 series (*Eggleton* and *Davies*) (all in BMNH).

## *Amicotermes dibogi* sp. n.

(Figs 62–75, 176)

Head capsule pale yellow or yellow, antennal flagellum, colour of darkest part, yellow or pale yellow-brown, pronotum yellow-white or pale yellow, legs pale yellow, abdominal tergites hyaline.

Head capsule circular to oval, setae sparse, emergent, longest setae more or less regularly and symmetrically arranged. Fontanelle absent. Fore coxae usually with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed or much smaller than the other two.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior margin of right first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting to left of nerve cord in ventral view, proctodeal first segment very long, over eight times proximal width, dilated to about twice its basal width throughout length, lateral displacement of enteric valve in unopened abdomen to left of heart in dorsal view; enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, unsclerotised or colourless throughout with very elongated tapered spines, the largest numbering up to 14, straight and evenly tapered, shorter than or equal to least width of ridges in position

three, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; subsidiary armature on one or more of enteric valve ridges with prominent spines smaller than main armature, covering entire ridge surface, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly, armed with very sparse, scattered minute spines or spicules.

*Measurements and diagnostic ratios* [12 individuals from 3 series]:

Head capsule width 0.656 to 0.701 mm (mean 0.676 SD 0.014).
Postclypeus width 0.324 to 0.362 mm (mean 0.347 SD 0.011).
Postclypeus length 0.192 to 0.227 mm (mean 0.206 SD 0.012).
Left mandible index 0.801 to 0.902 (mean 0.852).
Right mandible index 0.973 to 1.295 (mean 1.101).
Right second marginal index 0.788 to 1.262 (mean 0.994).
Right first to second marginal index 1.458 to 1.783 (mean 1.632).
Pronotum width 0.440 to 0.489 mm (mean 0.470 SD 0.015).
Pronotum length 0.192 to 0.227 mm (mean 0.206 SD 0.012).
Hind tibia length 0.659 to 0.730 mm (mean 0.703 SD 0.018).
Fore tibia length 0.576 to 0.618 mm (mean 0.594 SD 0.013).
Fore tibia thickness 0.127 to 0.148 mm (mean 0.139 SD 0.006).
Fore tibial index (length over width) 3.952 to 4.759 (mean 4.272).
Left mandible, complex ratio La divided by L1.Lm 18.009 to 23.312 (mean 20.937).
Right mandible, complex ratio Ra divided by R1.Rm 20.653 to 30.758 (mean 23.927).

COMPARISONS. *A. dibogi* has already been compared individually with the species that precede it; however, it is so distictive with its long, dilated P1 that pushes the enteric valve seating into a left dorsal position and the finely spiny and spiculate enteric valve armature, that it does not need detailed comparisons with the remaining species under its own heading. Although distinct from the other species of the genus in the characters specified, it is not so widely different as to require separation in another genus.

MATERIAL EXAMINED. [total 7 series]
Holotype worker and Paratypes from Type series (field collection no. $H_2C$-1), **Cameroon**: Mbalmayo Forest Reserve, Ekombitie, Aug. 1997 (*Eggleton et al.*); other Paratype material, Ekombitie, Aug. 1995, Nov. 1995, July 1996, Aug. 1997, Ebogo, Feb. 1996 (*Eggleton et al.*) (all in BMNH).This species is named in honour of Dr. Luc Dibog, a member of the TIGER team, who was first to recognise that it was a distinct species on the strength of its enteric valve armature and long first proctodeal segment.

## *Amicotermes galenus* Sands, 1972 [Type species]

(Figs 76–82, 177, 178)

Head capsule yellow, antennal flagellum, colour of darkest part, pronotum and legs, yellow-white or pale yellow, abdominal tergites yellow-white.

Head capsule circular, setae sparse, emergent, longest setae randomly scattered. Fontanelle absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior margin of first marginal tooth equal in length to that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than or approximately equal in size to outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on ridges one and two numbering 1–9, those on ridges three numbering 10–14, and on ridge four, up to 14, straight and evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size; subsidiary armature on ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined; membranous wall of enteric valve between and beyond ridges scaly, armed with minute spicules, numerous but not dense, scattered, fringing scales proximally.

*Measurements and diagnostic ratios* [1 individual]:

Head capsule width 0.763 mm.

Postclypeus width 0.425 mm.
Postclypeus length 0.25 mm.
Left mandible index 1.092.
Right mandible index 1.329.
Right second marginal index 0.957.
Right first to second marginal index 1.793.
Pronotum width 0.485 mm.
Pronotum length 0.269 mm.
Hind tibia length 0.725 mm.
Fore tibia length 0.563 mm.
Fore tibia thickness 0.13 mm.
Fore tibial index (length over width) 4.327.
Left mandible, complex ratio La divided by L1.Lm 26.495.
Right mandible, complex ratio Ra divided by R1.Rm 31.280.

COMPARISONS. *A. galenus* has already been compared with the preceding species. *A. gasteruptus* is smaller with lower mandible indices and has the front edge of the right first marginal tooth equal in length to that of the second; the largest apical spines of the main enteric valve armature are curved on a tri-radially symmetrical valve. *A. ivorensis* is again smaller with lower mandible indices and has the left first marginal tooth roughly equilateral; it lacks prominent fore coxal setae; the largest apical spines of the enteric valve main armature are less numerous on a tri-radially symmetrical valve with very sparse subsidiary armature. *A. mayombei* is also smaller, with lower mandible indices and has the front edge of the left third marginal tooth equal to that of the first, while the fourth marginal reaches the side of the molar prominence; the largest apical spines of the main enteric valve armature are curved and shorter than or equal to the least width of ridges three. *A. mbalmayoensis* is larger, lacks prominent fore coxal setae and has well developed fore tibial apical spurs; the left first marginal tooth is roughly equilateral while the fourth marginal reaches the side of the molar prominence; the largest apical spines of the main enteric valve armature are shorter than or equal to the least width of ridges three and the subsidiary armature consists of small single spines on scales, the valve symmetry being hexa-radial. *A. multispinus* is smaller with lower mandible indices and has the left first marginal tooth roughly equilateral while the fourth marginal reaches the side of the molar prominence; the front edge of the right first marginal tooth is shorter than that of the second; the largest apical spines of the main enteric valve armature are curved on a tri-radially symmetrical valve and much more numerous on ridges one and three. *A. spiculatus* is smaller, with lower main mandible indices and has the left first marginal tooth roughly equilateral while the front edge of the left third marginal tooth is equal to that of the first; it has well developed fore tibial apical spurs; the largest apical spines of the main enteric valve armature are conical and shorter than the least width of ridges three, while the differential sclerotisation of the valve ridges is characteristic.

MATERIAL EXAMINED.
**Democratic Republic of Congo**: Katanga, Keyburg near Elizabethville, 1948 single Paratype from Type series, in the Natural History Museum, London (*Emerson*). (Holotype imago and other Paratypes in American Museum of Natural History, examined and designated at the time of the first description).

## *Amicotermes gasteruptus* sp. n.

(Figs 83–98, 179)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, yellow or pale yellow-brown, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular or oval, setae sparse, the emergent, longest setae randomly scattered. Fontanelle present as pale spot or absent. Fore coxae without prominent larger setae or with four or more prominent larger setae arranged in line or group on anterior surface; fore tibial apical spurs numbering three, third well developed, at least half the size of the others or much smaller than the other two.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior or approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view with proximal end clear of or just reaches side of molar prominence. Right mandible, anterior edge of first marginal tooth shorter.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length; lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view; enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, sclerotised at distal ends, pale brown or yellow-brown; main armature with very elongated tapered spines, the largest apical spines on ridges one and three numbering 10–20, those on ridges two and four numbering 1–9; longest spines curved but still evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature, on scales or reticulations with indistinct vague or incomplete outlines, the spines being graduated, becoming longer towards distal end of ridge; membranous wall of enteric valve between and beyond

ridges scaly, armed with numerous but not dense, scattered, minute spines or spicules fringing scales proximally.

*Measurements and diagnostic ratios* [11 individuals from 5 series]:
Head capsule width 0.598 to 0.635 mm (mean 0.620 SD .011).
Postclypeus width 0.301 to 0.339 mm (mean 0.322 SD 0.013).
Postclypeus length 0.166 to 0.205 mm (mean 0.184 SD 0.013).
Left mandible index 0.751 to 0.935 (mean 0.818).
Right mandible index 0.895 to 1.228 (mean 1.015).
Right second marginal index 0.796 to 1.097 (mean 0.987).
Right first to second marginal index 1.561 to 1.838 (mean 1.705).
Pronotum width 0.390 to 0.424 mm (mean 0.408 SD 0.01).
Pronotum length 0.168 to 0.246 mm (mean 0.200 SD 0.020).
Hind tibia length 0.597 to 0.6436 mm (mean 0.622 SD 0.014).
Fore tibia length 0.495 to 0.535 mm (mean 0.518 SD 0.011).
Fore tibia thickness 0.131 to 0.154 mm (mean 0.139 SD 0.006).
Fore tibial index (length over width) 3.393 to 3.876 (mean 3.726).
Left mandible, complex ratio La divided by L1.Lm 20.184 to 28.664 (mean 23.214).
Right mandible, complex ratio Ra divided by R1.Rm 20.67 to 30.394 (mean 24.89).

COMPARISONS. *A. gasteruptus* has already been compared with the preceding species. It forms a terminal pair with *A. autothysius* in all of the trees apart from the Saitou and Nei tree and is close to it in the ordination. *A. ivorensis* is a little larger and has the front edge of the right first marginal tooth equal to that of the second; the apical spines of the enteric valve main armature are fewer in number on ridges one and three, while the subsidiary armature is very sparse. *A. mayombei* appears closely related, but the front edge of the left third marginal is roughly equal to that of the first; the longest apical spines of the enteric valve main armature are shorter than or equal to the least width of ridges three and on ridge one number less than ten, the valve symmetry being bilateral. *A. mbalmayoensis* is much larger and the longest spines of the main enteric valve armature are shorter than or equal to the least width of ridges three, while the subsidiary armature consists of small single spines on scales, the symmetry being hexa-radial. *A. multispinus* is very slightly larger and has more numerous apical spines on ridges one and three of the enteric valve main armature. *A. spiculatus* is much larger with proportionately longer legs; its enteric valve ridges are ellipsoid, not 'waisted' and bear straight apical spines, while the symmetry of the valve is bilateral owing to differential sclerotisation of the ridges.

MATERIAL EXAMINED. [total 9 series]
Holotype worker and Paratypes from Type series (field collection no. 38P-1) **Cameroon**: Mbalmayo Forest Reserve, Ebogo, Feb. 1996 (*Eggleton et al.*); other Paratype material, Eboufek, 5 series, Bilik, July–Aug. 1992, Ekombitie, Nov. 1995, Ebogo, Mar. 1996 (*Eggleton et al.*) (all in BMNH).

## *Amicotermes ivorensis* sp. n.

(Figs 99–110, 180)

Head capsule, antennal flagellum, colour of darkest part, pronotum and legs, pale yellow, abdominal tergites yellow-white.

Head capsule circular or short oval near circular, setae sparse, emergent, longest setae randomly scattered. Fontanelle present as pale spot or small depression. Fore coxae without prominent larger setae on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth equal in length to that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines or distinctly 'waisted' at their base, then wider, all ridges weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on each ridge numbering 1–9, straight or curved but still evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with backwardly directed indistinct scales, outlines vague or incomplete, fringed with very sparse small spines or spicules or small single backwardly directed spines, the latter graduated, becoming longer towards distal end of ridge; membranous wall of enteric

valve between and beyond ridges smooth, armed with very sparse scattered minute spicules.

*Measurements and diagnostic ratios* [3 individuals from 1 series]:

Head capsule width 0.657 to 0.713 mm (mean 0.684 SD 0.028).
Postclypeus width 0.359 to 0.381 mm (mean 0.368 SD 0.011).
Postclypeus length 0.205 to 0.241 mm (mean 0.227 SD 0.019).
Left mandible index 0.824 to 0.953 (mean 0.889).
Right mandible index 0.947 to 1.149 (mean 1.061).
Right second marginal index 0.839 to 1.136 (mean 0.969).
Right first to second marginal index 1.743 to 1.998 (mean 1.829).
Pronotum width 0.429 to 0.468 mm (mean 0.445 SD 0.020).
Pronotum length 0.206 to 0.293 mm (mean 0.252 SD 0.044).
Hind tibia length 0.665 to 0.692 mm (mean 0.680 SD 0.014).
Fore tibia length 0.525 to 0.549 mm (mean 0.540 SD 0.014).
Fore tibia thickness 0.135 to 0.148 mm (mean 0.142 SD 0.007).
Fore tibial index (length over width) 3.696 to 3.890 (mean 3.818).
Left mandible, complex ratio La divided by L1.Lm 21.554 to 24.308 (mean 22.474).
Right mandible, complex ratio Ra divided by R1.Rm 23.91to 27.495 (mean 25.224).

COMPARISONS. *A. ivorensis* has already been compared with the preceding species. It stands somewhat isolated in the ordination, but is closest to *A. galenus* and *A. mbalmayoensis* in the consensus tree while variously attached in the other, phenetic trees. *A. mayombei* has prominent fore coxal setae, the left third margional tooth with its front edge equal in length to that of the first and the fourth marginal just reaching the side of the molar prominence, while the front edge of the right first marginal is shorter than that of the second; the longest apical spines of the enteric valve main armature are curved and shorter than or equal to the least width of ridges three, the valve being bilaterally symmetrical. *A. mbalmayoensis* is considerably larger with much longer legs, while the proximal end of the left fourth marginal tooth just reaches or is hidden behind the molar prominence and the front edge of the right first marginal is shorter than that of the second; the longest apical spines of the enteric valve main armature are more numerous and shorter than the least width of ridges three, the valve being hexa-radially symmetrical. *A. multispinus* has prominent fore coxal setae, the left third marginal tooth with its front edge equal in length to that of the first and the fourth marginal just reaching the side of the molar prominence, while the front edge of the right first marginal is shorter than that of the second; the ridges of the main enteric valve armature have more numerous apical spines. Finally, *A. spiculatus* has much longer legs with prominent fore coxal setae and the left third marginal tooth with its front edge equal in length to that of the first, while the front edge of the right first marginal is shorter than that of the second; the largest apical spines of the main enteric valve armature are conical, shorter than the least width of ridges three, and more numerous on a bilaterally symmetrical valve with differential sclerotisation of the ridges.

MATERIAL EXAMINED. [one series]
Holotype worker and Paratypes from Type series, **Ivory Coast**: near Ndouci in forest, 1969 (*Josens*) (all in BMNH).

## *Amicotermes mayombei* sp. n.

(Figs 111–124, 181, 182)

Head capsule, antennal flagellum, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular or oval, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior margin of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, sclerotised at distal end, pale brown or yellow-brown with very elongated tapered spines, the largest on ridges one, two and four numbering up to 10, those on ridges three 10–20, longest spines curved but still evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size; subsidiary armature on one or more of enteric valve ridges with

scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly armed with short spicules, dense distally, fringing scales proximally.

*Measurements and diagnostic ratios* [14 individuals from 6 series]:

Head capsule width 0.614 to 0.713 mm (mean 0.651 SD 0.028).
Postclypeus width 0.322 to 0.373 mm (mean 0.344 SD 0.014).
Postclypeus length 0.162 to 0.214 mm (mean 0.185 SD 0.014).
Left mandible index 0.772 to 0.984 (mean 0.888).
Right mandible index 0.921 to 1.307 (mean 1.138).
Right second marginal index 0.936 to 1.169 (mean 1.047).
Right first to second marginal index 1.461 to 1.932 (mean 1.638).
Pronotum width 0.382 to 0.448 mm (mean 0.408 SD 0.018).
Pronotum length 0.175 to 0.22 mm (mean 0.191 SD 0.012).
Hind tibia length 0.637 to 0.736 mm (mean 0.683 SD 0.027).
Fore tibia length 0.499 to 0.571 mm (mean 0.542 SD 0.019).
Fore tibia thickness 0.133 to 0.145 mm (mean 0.139 SD 0.005).
Fore tibial index (length over width) 3.759 to 4.028 (mean 3.912).
Left mandible, complex ratio La divided by L1.Lm 18.707 to 26.77 (mean 22.184).
Right mandible, complex ratio Ra divided by R1.Rm 21.009 to 29.644 (mean 25.813).

COMPARISONS. *A. mayombei* has already been compared with the preceding species. In most of the phenetic trees it joins *A. autothysius* and *A. gasteruptus* at a slightly lower phenon level and in the strict consensus tree it links with them at node 14. *A. mbalmayoensis* is considerably larger and lacks prominent fore coxal setae while the left first marginal tooth is approximately equilateral; The enteric valve ridges are tapering ellipsoid bearing straight spines and the valve is hexa-radially symmetrical. *A. multispinus* is a little smaller and has the left first marginal tooth aproximately equilateral; the longest apical spines of the main enteric valve armature are more numerous on ridges one and three and longer than the least width of three, while the symmetry of the valve is tri-radial. In *A. spiculatus* the legs are distinctly longer, the left first marginal tooth is equilateral and the fourth marginal is clear of the molar prominence; the enteric valve ridges are tapering ellipsoid, not 'waisted' and differentially sclerotised, ridge one being colourless while ridges three and four are pale brown, two being intermediate; the largest apical spines are straight and conical.

MATERIAL EXAMINED. [total 5 series]
Holotype worker and Paratypes from Type series (field collection no. T1.10) **Congo (Brazzaville)**: Mayombe, Feb. 1997 (*Eggleton* and *Davies*); other Paratype material, Feb.1997, 4 series (*Eggleton* and *Davies*) (all in BMNH).

## *Amicotermes mbalmayoensis* sp. n.

(Figs 125–137, 183, 184)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, yellow or pale yellow-brown, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae numerous but not dense, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae without prominent larger setae on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than or equal in length to that of first, fourth marginal tooth in front view just reaches side of or with proximal end hidden behind molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width tubular throughout its length, lateral dis-placement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on each ridge numbering 10–14, straight and evenly tapered, shorter than or equal to least width of ridges in position three; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse small single backwardly directed spines on scales, more or less uniform throughout length of ridge, scales or reticulations indistinct, outlines vague or incomplete; symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; membranous wall of enteric valve between and beyond ridges scaly, armed with minute spicules, dense distally, fringing scales proximally.

*Measurements and diagnostic ratios* [9 individuals from 3 series]:

Head capsule width 0.765 to 0.800 mm (mean 0.781 SD 0.013).
Postclypeus width 0.413 to 0.434 mm (mean 0.424 SD 0.008).
Postclypeus length 0.199 to 0.239 mm (mean 0.215 SD 0.012).
Left mandible index 0.896 to 0.978 (mean 0.944).
Right mandible index 1.065 to 1.366 (mean 1.174).
Right second marginal index 0.88 to 1.245 (mean 1.013).
Right first to second marginal index 1.606 to 1.987 (mean 1.811).
Pronotum width 0.523 to 0.582 mm (mean 0.545 SD 0.019).
Pronotum length 0.230 to 0.267 mm (mean 0.252 SD 0.013).
Hind tibia length 0.779 to 0.82 mm (mean 0.796 SD 0.014).
Fore tibia length 0.614 to 0.677 mm (mean 0.651 SD 0.019).
Fore tibia thickness 0.159 to 0.173 mm (mean 0.166 SD 0.005).
Fore tibial index (length over width) 3.602 to 4.078 (mean 3.916).
Left mandible, complex ratio La divided by L1.Lm 22.319 to 27.038 (mean 23.941).
Right mandible, complex ratio Ra divided by R1.Rm 20.164 to 26.881 (mean 24.080).

COMPARISONS. *A. mbalmayoensis* has already been compared with the preceding species. *A. multispinus* is much smaller and has prominent fore coxal setae; the front edge of the left third marginat tooth is equal in length to that of the first and the right mandible first to second marginal index is lower; the enteric valve ridges are 'waisted' at the base of the apical spines which are curved, longer than the least width of ridges three and more numerous on ridges one and three, the valve being tri-radial. *A. spiculatus* is smaller with a lower left mandible index; the apical spines of the enteric valve main armature are conical and more numerous on ridges three which are differentially sclerotised along with four, while one is unsclerotised and two intermediate, the valve being bilaterally symmetrical.

MATERIAL EXAMINED. [total, 3 series]
Holotype worker and Paratypes from Type series (field collection no. $H_3$P.2) **Cameroon**: Mbalmayo Forest Reserve, Ekombitie, Nov. 1996 (*Eggleton et al.*); other *Paratypes*, Ekombitie, Nov. 1995, Ebogo, Mar. 1996 (*Eggleton et al.*) (all in BMNH).

## *Amicotermes multispinus* sp. n.

(Figs 138–150, 185)

Head capsule, antennal flagellum, colour of darkest part, pronotum and legs, yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular, throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on ridge one numbering 15–20, those on ridges two and four numbering 1–9, those on ridges three numbering 15 to over 20, the longest, curved but still evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines becoming longer towards distal end of ridge, scales or reticulations indistinct, outlines vague or incomplete; membranous wall of enteric valve between and beyond ridges scaly, armed with numerous but not dense, scattered, short spicules fringing scales proximally.

*Measurements and diagnostic ratios* [3 individuals from 1 series]:

Head capsule width 0.642 to 0.647 mm (mean 0.645).
Postclypeus width 0.334 to 0.356 mm (mean 0.342).
Postclypeus length 0.183 to 0.191 mm (mean 0.186).
Left mandible index 0.802 to 0.903 (mean 0.852).
Right mandible index 1.049 to 1.163 (mean 1.100).
Right second marginal index 0.924 to 1.021 (mean 0.974).
Right first to second marginal index 1.569 to 1.594 (mean 1.581).

Pronotum width 0.412 to 0.436 mm (mean 0.427).
Pronotum length 0.183 to 0.191 mm (mean 0.186).
Hind tibia length 0.624 to 0.629 mm (mean 0.626).
Fore tibia length 0.525 to 0.531 mm (mean 0.528).
Fore tibia thickness 0.134 to 0.141 mm (mean 0.138).
Fore tibial index (length over width) 3.732 to 3.974 (mean 3.834).
Left mandible, complex ratio La divided by L1.Lm 23.999 to 27.622 (mean 25.824).
Right mandible, complex ratio Ra divided by R1.Rm 23.347 to 26.271 (mean 24.767).

COMPARISONS. *A. multispinus* has already been compared with all of the preceding species, only *A. spiculatus* remaining. The latter is slightly larger and has the left fourth marginal tooth clear of the molar prominence; the enteric valve ridges are tapering ellipsoid, not 'waisted', and differentially sclerotised with fewer, straight conical spines on ridges one and three, the valve being bilaterally symmetrical.

MATERIAL EXAMINED. [one series]
Holotype worker and Paratypes from Type series (field collection no. T1.20) **Congo (Brazzaville)**: Mayombe, Feb. 1997 (*Eggleton* and *Davies*) (all in BMNH).

### *Amicotermes spiculatus* sp. n.

(Figs 151–161, 186)

Head capsule pale yellow, antennal flagellum, colour of darkest part pale yellow or yellow, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule oval, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae with three or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, enteric valve ridge in position one unsclerotised or colourless throughout, positions two and four weakly sclerotised distally, pale yellow or yellow, position three sclerotised at distal end, pale brown or yellow-brown main armature of all ridges with large backwardly directed erect conical spines, those on ridges one and two numbering up to 14, on ridges three, 15–20 and on ridge four, 1–9, the longest being straight and evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size; subsidiary armature on one or more of enteric valve ridges with prominent spines different from or smaller than main armature, covering entire ridge surface, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations indistinct, outlines vague or incomplete; membranous wall of enteric valve between and beyond ridges scaly, armed with short scattered spicules, numerous but not dense, fringing scales proximally.

*Measurements and diagnostic ratios* [only two specimens available]:

Head capsule width 0.696 to 0.706 mm.
Postclypeus width 0.370 to 0.379 mm.
Postclypeus length 0.203 to 0.206 mm.
Left mandible index 0.855 to 0.88.
Right mandible index 1.069 to 1.149.
Right second marginal index 1.016 to 1.029.
Right first to second marginal index 1.788 to 1.813.
Pronotum width 0.438 to 0.460 mm.
Pronotum length 0.233 to 0.239 mm.
Hind tibia length 0.784 to 0.794 mm.
Fore tibia length 0.620 to 0.625 mm.
Fore tibia thickness 0.15 to 0.152 mm.
Fore tibial index (length over width) 4.119 to 4.135.
Left mandible, complex ratio La divided by L1.Lm 20.586 to 23.569.
Right mandible, complex ratio Ra divided by R1.Rm 24.213 to 25.340.

COMPARISONS. All the necessary comparisons of *A. spiculatus* have been made under the preceding species.

MATERIAL EXAMINED. [one series]
Holotype worker and one Paratype (field collection no. CHR 35–40) **Cameroon**: Ebolowa, Akok, June 1997, (*Eggleton et al.*) (all in BMNH).

## PHENETIC AND PHYLOGENETIC ANALYSIS

The purpose in undertaking these analyses was to examine the apparent relationships between the twelve species of the genus now recognised and their geographical distribution. Phenetics, that is the study of relationships based on overall similarity between taxa, has largely gone out of use in favour of cladistics because the methods take no account of homoplasy.

However, in a small, relatively homogeneous set of species such as this, where convergence was thought unlikely to be a major feature, they offered an alternative way of looking at the character matrix. In practice, it can be seen from the relatively low values of the consistency and retention indices of the Hennig strict consensus tree, and the character states marked on it that there was more homoplasy than might have been expected. The precise topography of the individual trees depends on differences in the algorithms that define them, and there is no clear 'best' tree, although some taxonomists would claim this role for the Hennig tree. Where a cluster of species is robust through several methods including the cladistic format, it seems likely that the underlying relationships are more clearly illustrated.

The DELTA file of *Amicotermes* was converted by means of the PANKEY programmes SC3 and DELPAUP1 respectively into a matrix of similarity coefficients for input to NTSYS (Rohlf, 1993) phenetics and Principal Coordinates analyses and a coded character matrix for HENNIG86 (Farris 1988) phylogenetic analysis. *Acholotermes* was included as an outgroup, being the most closely related other genus. The first analyses were based on the original DELTA file, but because that included ranges of variation in the character codings, many of the characters were represented by queries in the HENNIG matrix. Since measurements had proved important in distinguishing some of the species, it was undesirable they should be inactive in the study of relationships. In order to avoid this, the variable characters were recoded to their median (in multi-states) or mean values (in continuous variables). In the latter case, the DELTA file included the facility to allocate measurements or ratios to KEY STATES, equal sub-divisions of the total range of each variable. It was observed that for these, closely similar members of the same genus the variances were roughly equal and it was not thought necessary to standardise the data. In practice this amounted to a crude form of gap coding for the morphometrics. Most of the characters then became fully active, but the effects of this procedure turned out to be comparatively slight in terms of the branching of trees and the positions of terminal taxa. The results of both phylogenetic and phenetic analysis are shown in Figs 162–168.

The strict consensus tree derived from the most parsimonious two Hennig trees (Fig. 162) has essentially the same topology as one of them. The states of those characters with retention indices greater than 50 are marked on the tree at each node; in addition, the tree also indicates the autapomorphies of individual taxa on their stems. It places *A. dibogi* separated from the rest of the genus and close to the outgroup, *Acholotermes*, with a considerable range of autapomorphies. The character states shown at node 24 are the plesiomorphic states of the characters concerned on this particular tree. Succeeding single branches from low on the tree are occupied by *A. camerunensis, A. spiculatus* and *A. cristatus*, which show progressive development and localisation of straight spiny armature of the enteric valve. The rest of the species appeared to divide into two groups, one of three (*A. mbalmayoensis, A. ivorensis* and *A. galenus*) and one of five (*A. multispinus*, *A. congoensis, A. mayombei, A. gasteruptus* and *A. autothysius*), the two last named forming a terminal pair, with *A. congoensis* and *A. multispinus* joining the group at slightly lower levels. The lower nodes of the tree are determined largely by features of the main armature of the enteric valve, while above node 19, measurement characters predominate. However, the shape of the enteric valve ridges ('waisted', 23a) and the type of spines in the main armature (elongated, curved taper, 36a) are important synapomorphies at node 18 that define the group of five species mentioned above; they also suggest a trend towards certain other genera such as *Ateuchotermes* and perhaps *Apagotermes*.

The Principal Coordinates plot (Fig. 163) shows the positions of the taxa in relation to the first three eigenvectors of the similarity matrix transformed by double centering. *A. dibogi* is again widely separated on vectors one and two from the other species and placed near to the outgroup. *A. camerunensis, A. spiculatus* and *A. cristatus* are separated on vectors two and three while most of the separation of *A. mbalmayoensis, A. ivorensis* and *A. galenus* is accounted for by vector three. *A. congoensis* is also separated mainly on V3 while the remaining two pairs are relatively close together on all three vectors. The minimum spanning tree is superimposed on the ordination in order to show up any local distortions. It links the outgroup to *A. dibogi* which in turn is linked to *A. autothysius*, *A. gasteruptus* and *A. mayombei* in series. It then branches to *A. cristatus*, *A. spiculatus* and *A. camerunensis* in turn and to *A. multispinus* and *A. congoensis*, with further branches to *A. mbalmayoensis* and *A. galenus*, which is finally linked to *A. ivorensis*.

The various SAHN phenetic clustering methods, (Single (Fig. 164), Flexible (Fig. 165) and Complete (Fig. 166) Linkage methods and Unweighted pair-group method of averages (Fig. 167)) based on the matrix of similarity coefficients give comparable results, allowing for a small amount of branch-swapping, in terms of the terminal groups of taxa, to the HENNIG86 (Farris, 1988) tree. *A. dibogi* is always separate and near to *Acholotermes*, the successive additions at lower levels are largely similar, and the two terminal groups also retain their cohesion to a certain extent. The Single-linkage tree, with its tendency to form long chain clusters, has the *A. autothysius–A. gasteruptus–A. congoensis–A. may-*

*ombei–A. multispinus* group but adds in *A. galenus* at about the 0.57 phenon level. The other group has broken up with *A. ivorensis* and *A. mbalmayoensis* separated; *A. spiculatus* and *A. cristatus* unite at the 0.53 phenon level. Both Flexible and Complete linkage methods keep *A. autothysius–A. gasteruptus–A. mayombei* together at about 0.55 phenon level and also *A. congoensis–A. multispinus–A. galenus* at 0.50 phenons. *A. spiculatus* and *A. cristatus* similarly combine, but Flexible linkage adds *A. camerunensis* at about 0.35 phenons and Complete linkage adds *A. ivorensis*. The UPGMA tree keeps *A. autothysius–A. gasteruptus–A. mayombei* together at about 0.58 phenon level and also *A. congoensis–A. multispinus–A. galenus* at 0.55 phenons; *A. spiculatus* and *A. cristatus* combine at 0.53, and *A. camerunensis* at 0.42. A strict consensus tree of the Complete and Flexible linkage methods only leaves the *A. mayombei–A. gasteruptus–A. autothysius* group recognisable, the rest being reduced to a comb and nothing remains if Single linkage is added in, while that of the UPGMA and Neighbour-joining trees apparently also leaves no grouping in common.

The only exception to the above arrangement occurs in the Saitou and Nei (1987) Neighbour-joining tree (Fig. 168), which uses an algorithm based on the principle of parsimony to produce from the dissimilarity matrix a 'phylogenetic' tree. Here the species closest to the outgroup is *A. gasteruptus*, while *A. dibogi* forms a terminal pair high up the tree with *A. cristatus*. Considering how far apart these two appear in the ordination of the first three vectors, it might be concluded that they come to be 'neighbours' as a result of closeness on other, lower level vectors that cannot be plotted; however, this is not borne out by their positions at almost the extreme ends on the minimum spanning tree, which agrees with both the cladistic and the other phenetic classifications in placing *A. dibogi* next to the outgroup. None of the terminal groups recognised in the other methods remains.

The results of the HENNIG, SAHN and ordination analyses all share aspects with an intuitive view of the probable relationships of most of the species. Perhaps the most interesting feature that is found in all of the trees apart from the Saitou and Nei tree is the distribution of taxa from each of the two regions sampled among the terminal groups. Each fauna appears to include representatives of the different trends within the genus, and it would be interesting to see whether this were to be maintained through further sampling on a wider geographical basis. A surprise is the apparently close relationship of *A. dibogi* to the outgroup which must be a reflection of its relatively unspecialised, hexa-radially symmetrical, finely spiny and spiculate enteric valve armature. Other, apparently derived features of the gut, such as the elongated and dilated P1, which pushes the enteric valve seating into a dorsal position, only account for three 'characters' out of the total set of 60 and they appear as autapomorphies on the tree. The Saitou and Nei is the only tree to place *A. dibogi* in a derived position distant from *Acholotermes*.

ACKNOWLEDGEMENTS I am grateful to Dr Paul Eggleton for reading and commenting on the manuscript of this paper, and to my colleagues in the Termite Group at The Natural History Museum for helpful discussions and testing the key to species. Thanks are also due to the Trustees of The Natural History Museum for permission to examine specimens in the collection.

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## APPENDIX

The entire DELTA file is shown below, except that the character states recorded for the species are omitted, since they have been converted to keys and descriptions. The symbols for character types are OM, ordered multistate and RN, real numbers, the default being unordered multistate. The format is rigid in that certain lines must end in a slash, and every line begins with a single space. the numbers of characters, states and items stated at the beginning must correspond exactly to those included in the file

*HEADING THE AFRICAN SOLDIERLESS TERMITE GENUS AMICOTERMES/
*SPECIAL STORAGE
*KEY OPTIONS OLDKEY PARTIAL /
*NUMBER OF CHARACTERS 60
*MAXIMUM NUMBER OF STATES 6
*MAXIMUM NUMBER OF ITEMS 13
*CHARACTER TYPES
1, OM 2, OM 3, OM 4, OM 5, OM 6, OM 11, OM 14, OM 16, OM 18, OM 24, OM 25, OM 26, OM 27, OM 28, OM 29, OM 30, OM 31, OM 32, OM 33, OM 34, OM 35, OM 38, OM 40, OM 42, OM 45, OM 46, RN 47, RN 48, RN 49, RN 50, RN 51, RN 52, RN 53, RN 54, RN 55, RN 56, RN 57, RN 58, RN 59, RN 60, RN
*NUMBERS OF STATES
1, 4 2, 4 3, 3 4, 3 5, 3 6, 3 11, 3 14, 3 15, 3 16, 3 18, 3 24, 3 25, 3 26, 3 27, 3 28, 3 29, 3 30, 3 31, 3 32, 4 33, 4 34, 4 35, 4 38, 5 40, 3 42, 3 45, 3
*KEY STATES
46, 0.565–0.604/0.605–0.644/0.645–0.683/0.684–0.722/0.723–0.761/0.762–0.800
47, 0.300–0.333/0.334–0.367/0.368–0.401/0.402–0.434
48, 0.154–0.178/0.179–0.202/0.203–0.227/0.228–0.250
49, 0.697–0.781/0.782–0.866/0.867–0.951/0.952–1.036/1.037–1.12/1.121–1.205
50, 0.879–0.962/0.963–1.044/1.045–1.127/1.128–1.209/1.21–1.291/1.292–1.374
51, 0.788–0.867/0.868–0.946/0.947–1.025/1.026–1.104/1.105–1.183/1.184–1.262
52, 1.350–1.474/1.475–1.598/1.599–1.722/1.723–1.846/1.847–1.97/1.971–2.094
53, 0.375–0.426/0.427–0.478/0.479–0.53/0.531–0.582
54, 0.168–0.199/0.2–0.231/0.232–0.262/0.263–0.293
55, 0.565–0.629/0.63–0.693/0.694–0.756/0.757–0.820
56, 0.489–0.536/0.537–0.583/0.584–0.63/0.631–0.677
57, 0.127–0.147/0.148–0.166/0.167–0.185/0.186–0.205
58, 2.953–3.255/3.256–3.556/3.557–3.857/3.858–4.157/4.158–4.458/4.459–4.759
59, 17.556–22.634/22.635–27.712/27.713–32.789/32.79–37.867
60, 20.164–23.626/23.627–27.087/27.088–30.549/30.55–34.010
*CHARACTER DESCRIPTIONS
#1. head capsule <colour>/
1. yellow-white/
2. pale yellow/
3. yellow/
4. pale yellow-brown/

#2. antennal flagellum <colour of darkest part>/
1. yellow-white/
2. pale yellow/
3. yellow/
4. pale yellow-brown/

#3. pronotum <colour>/
1. yellow-white/
2. pale yellow/
3. yellow/

#4. legs <colour>/
1. yellow-white/
2. pale yellow/
3. yellow/

#5. abdominal tergites <colour>/
1. hyaline/
2. yellow-white/
3. pale yellow/

#6. head capsule <shape>/
1. circular/
2. short oval near circular/
3. oval/

#7. head capsule setae/
1. sparse/
2. numerous but not dense/

#8. head capsule emergent, longest setae/
1. randomly scattered/
2. regularly and symmetrically arranged/

#9. fontanelle/
1. present as pale spot or small depression/
2. absent/

#10. postclypeus <contour>/
1. clearly inflated/
2. strongly inflated, bulging, length more than half width at ginglymi/

#11. fore coxae/
1. without prominent larger setae on anterior surface/
2. with one to three prominent larger setae on anterior surface/
3. with four or more prominent larger setae arranged in line or group on anterior surface/

#12. fore tibial apical spurs/
1. numbering three, third well developed, at least half the size of the others/
2. numbering three, but third much smaller than the other two/

#13. left mandible, first marginal tooth/
1. with anterior edge distinctly longer than posterior/
2. approximately equilateral/

#14. left third marginal tooth with anterior edge/
1. shorter than that of first/
2. equal in length to that of first/
3. longer than that of first/

#15. left fourth marginal tooth in front view/
1. with proximal end clear of molar prominence/
2. just reaches side of molar prominence/
3. with proximal end hidden behind molar prominence/

#16. anterior margin of right first marginal tooth/
1. longer than that of second/
2. equal in length to that of second/
3. shorter than that of second/

#17. right first marginal tooth with exposed posterior edge/
1. equal to that of second marginal/
2. longer than that of second marginal/

#18. junction of mesenteron and proctodeum/
1. starting to left of nerve cord in ventral view/
2. starting beneath nerve cord in ventral view/
3. starting to right of nerve cord in ventral view/

#19. proctodeal first segment <length>/
1. shorter, up to eight times proximal width/
2. very long, over eight times proximal width/

#20. proctodeal first segment beyond junction with mesenteron <condition>/
1. tubular or conical throughout its length/
2. dilated to about twice its basal width throughout length/

#21. lateral displacement of enteric valve in unopened abdomen/
1. to left of heart in dorsal view/
2. to right of heart in dorsal or to left of nerve cord in ventral view/

#22. enteric valve 'seating' third lobe <size>/
1. smaller than outer pair/
2. approximately equal in size to outer pair/

#23. enteric valve ridges, <shape>/
1. more or less tapering ellipsoid to base of apical spines/
2. distinctly 'waisted' at base of apical spines, then wider/

#24. enteric valve ridge in position one/
1. sclerotised at distal end, pale brown or yellow-brown/
2. weakly sclerotised distally, pale yellow or yellow/
3. unsclerotised or colourless throughout/

#25. enteric valve ridges in position two/
1. sclerotised at distal end, pale brown or yellow-brown/
2. weakly sclerotised distally, pale yellow or yellow/
3. unsclerotised or colourless/

#26. enteric valve ridges in position three/
1. sclerotised at distal end, pale brown or yellow-brown/
2. weakly sclerotised distally, pale yellow or yellow/
3. unsclerotised or colourless/

#27. enteric valve ridge in position four/
1. sclerotised at distal end, pale brown or yellow-brown/
2. weakly sclerotised distally, pale yellow or yellow/
3. unsclerotised or colourless/

#28. main armature of enteric valve ridge in position one/
1. without large apical spines/
2. with large backwardly directed erect conical spines/
3. with very elongated tapered spines/

#29. main armature of enteric valve ridges in position two/
1. without large apical spines/
2. with large backwardly directed erect conical spines/
3. with very elongated tapered spines/

#30. main armature of enteric valve ridges in position three/
1. without large apical spines/
2. with large backwardly directed erect conical spines/
3. with very elongated tapered spines/

#31. main armature of enteric valve ridge in position four/
1. without large apical spines/
2. with large backwardly directed erect conical spines/
3. with very elongated tapered spines/

#32. largest apical spines on ridge one <of main armature, number>/
1. numbering 1–9/
2. numbering 10–14/
3. numbering 15–20/
4. numbering over 20/

#33. largest spines on ridges two <of main armature, number>/
1. numbering 1–9/
2. numbering 10–14/
3. numbering 15–20/
4. numbering over 20/

#34. largest spines on ridges three <of main armature, number>/
1. numbering 1–9/
2. numbering 10–14/
3. numbering 15–20/
4. numbering over 20/

#35. largest spines on ridge four <of main armature, number>/
1. numbering 1–9/
2. numbering 10–14/
3. numbering 15–20/
4. numbering over 20/

#36. longest spines of main armature <type>/
1. straight and evenly tapered/
2. curved but still evenly tapered/

#37. longest apical spines <length>/
1. longer than least width of ridges in position three at base of spines/
2. shorter than or equal to least width of ridges in position three/

#38. subsidiary armature on one or more of enteric valve ridges mainly/
1. reticulate/
2. with backwardly directed scales/
3. with backwardly directed scales fringed with small spines or spicules/

4. with small single backwardly directed spines on scales/
5. with prominent spines different from or smaller than main armature/

#39. subsidiary armature of enteric valve ridges/
1. with scales or reticulations well defined, distinct/
2. with scales or reticulations indistinct, outlines vague or incomplete/

#40. subsidiary armature of one or more of enteric valve ridges/
1. prominent, covering entire ridge surface/
2. scattered, somewhat sparse/
3. very sparse, few scales fringed with spines or spicules/

#41. subsidiary armature on one or more enteric valve ridges/
1. more or less uniform throughout length of ridge/
2. graduated, spines or spicules becoming longer towards distal end of ridge/

#42. symmetry of enteric valve armature/
1. more or less hexa-radial apart from slight differences in ridge size/
2. more or less tri-radial, alternate ridges reduced/
3. bilateral due to marked differences in spine and ridge size/

#43. membranous wall of enteric valve between and beyond ridges/
1. smooth/
2. scaly/

#44. membranous wall of enteric valve between and beyond ridges/
1. armed with minute spines or spicules/
2. armed with short spines or spicules/

#45. spines or spicules on membranous wall/
1. very sparse, scattered/
2. numerous but not dense, scattered, fringing scales proximally/
3. dense distally, fringing scales proximally/

#46. head capsule width <range, mean, SD>/ mm/

#47. postclypeus width <range, mean, SD>/ mm/

#48. postclypeus length <range, mean, SD>/ mm/

#49. left mandible index <range, mean>/

#50. right mandible index <range, mean>/

#51. right second marginal index <range, mean>/

#52. right first to second marginal index <range, mean>/

#53. pronotum width <range, mean, SD>/ mm/

#54. pronotum length <range, mean, SD>/ mm/

#55. hind tibia length <range, mean, SD>/ mm/

#56. fore tibia length <range, mean, SD>/ mm/

#57. fore tibia thickness <range, mean, SD>/ mm/

#58. fore tibial index (length over width) <range, mean>/

#59. left mandible, complex ratio La divided by L1.Lm <range, mean>/

#60. right mandible, complex ratio Ra divided by R1.Rm <range, mean>/

*ITEM DESCRIPTIONS

#1.Acholotermes <outgroup>/

#2.Amicotermes autothysius sp. n./

#3.Amicotermes camerunensis sp. n./

#4.Amicotermes congoensis sp. n./

#5.Amicotermes cristatus sp. n./

#6.Amicotermes dibogi sp. n./

#7.Amicotermes galenus Sands 1972/

#8.Amicotermes gasteruptus sp. n./

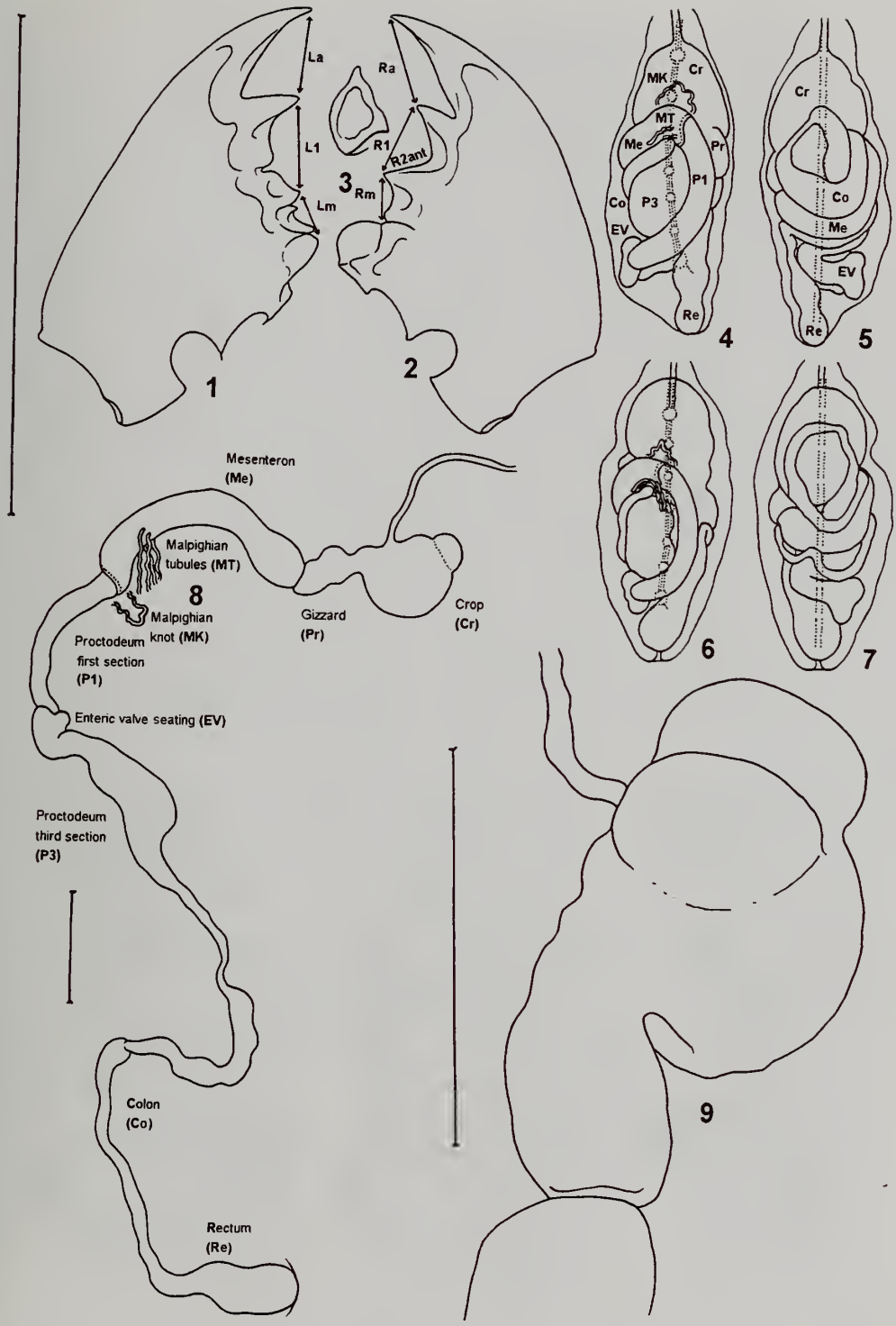
#9.Amicotermes ivorensis sp. n./

#10.Amicotermes mayombei sp. n./

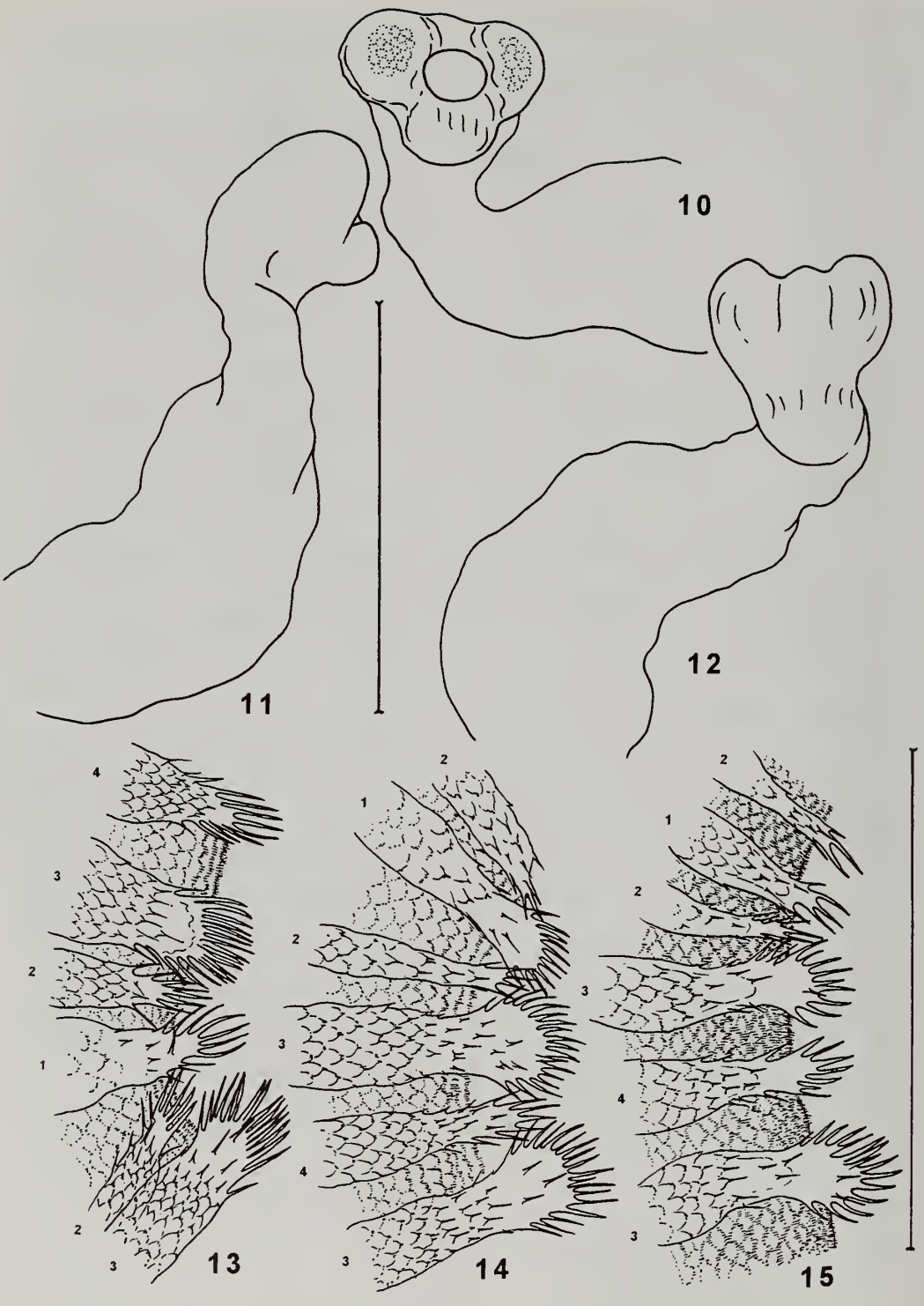
#11.Amicotermes mbalmayoensis sp. n./

#12.Amicotermes multispinus sp. n./

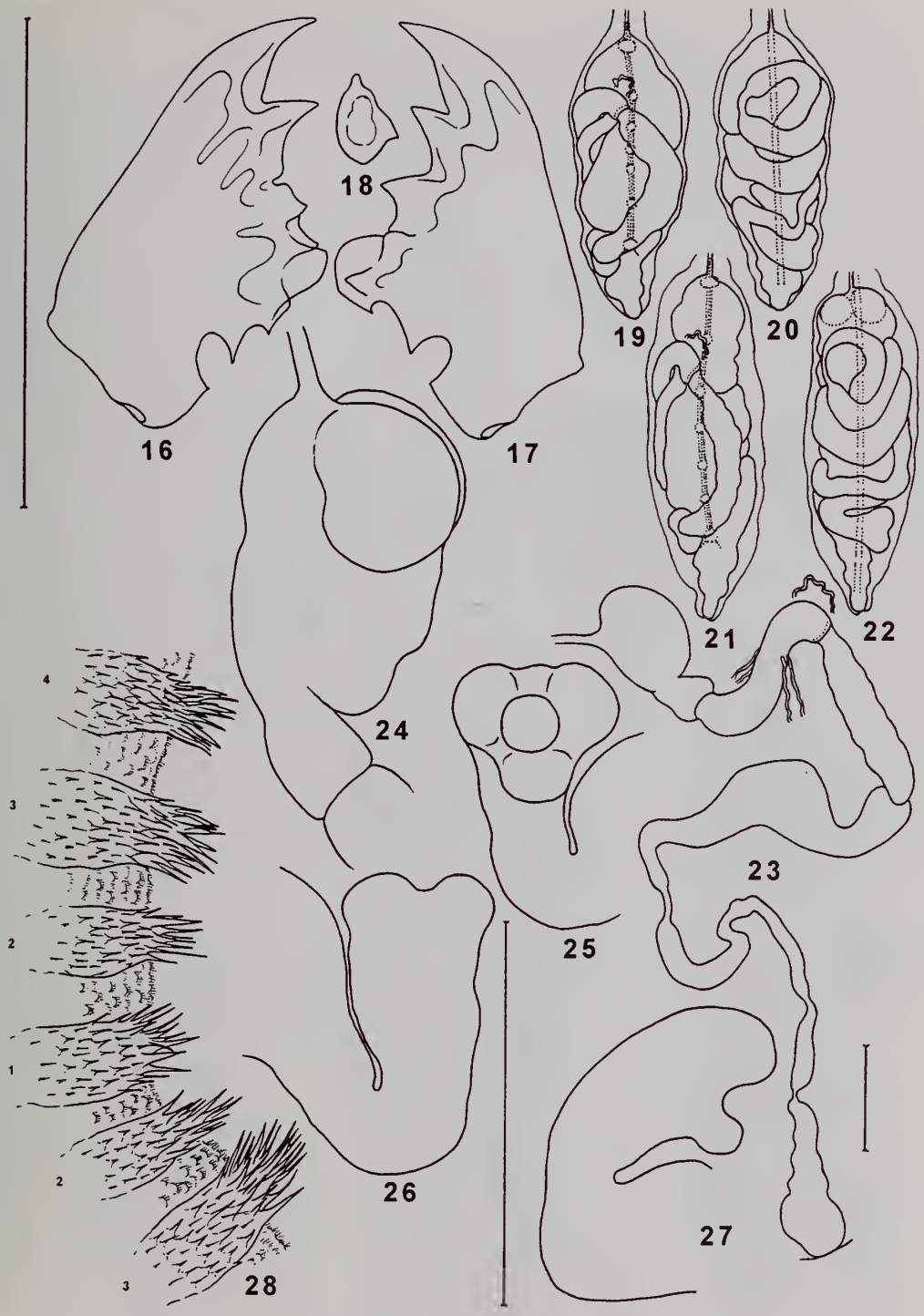
#13.Amicotermes spiculatus sp. n./



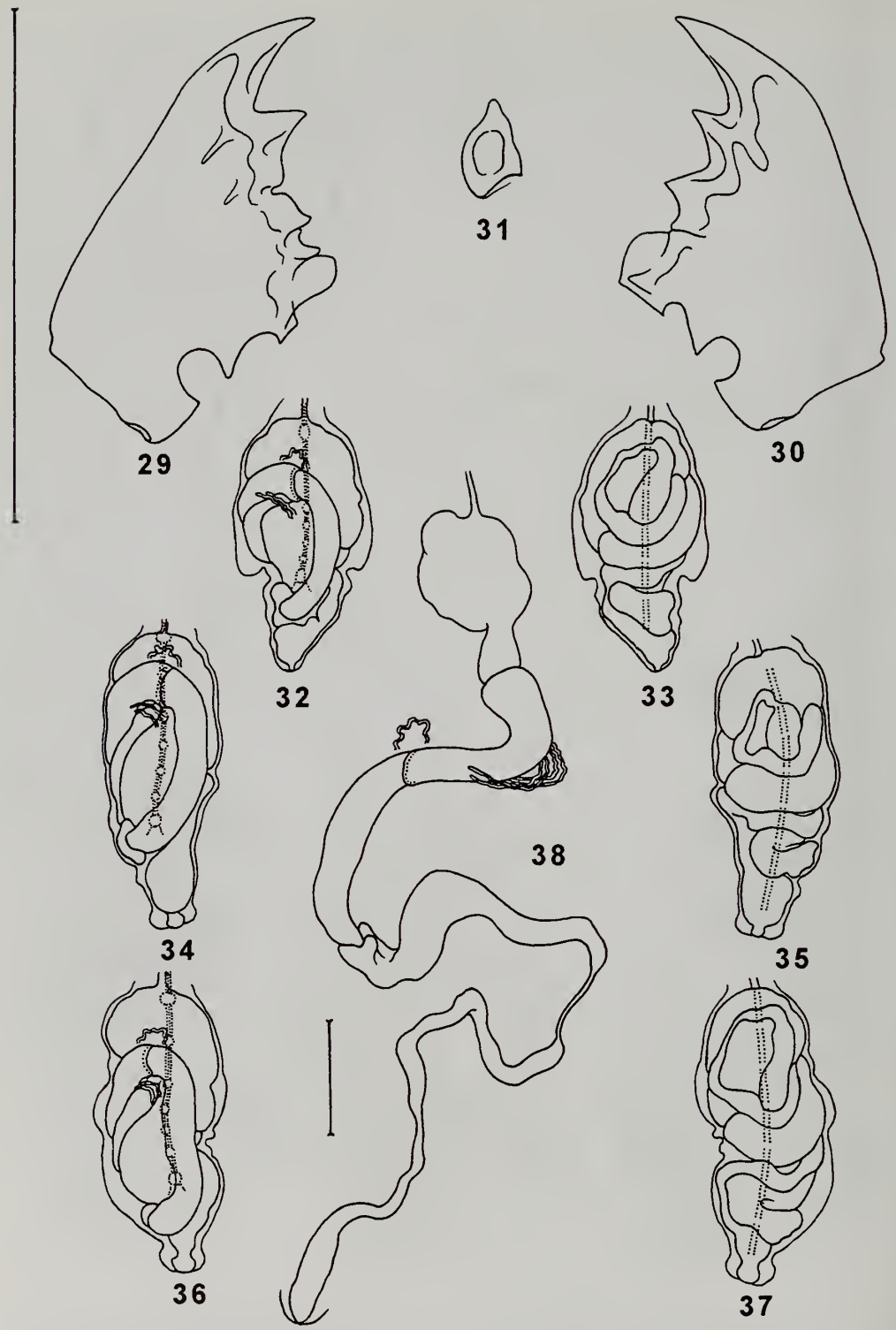

**Figs 1–9.** *Amicotermes autothysius.* 1–3, mandibles with surface view of right molar plate; 4, 6, ventral and 5, 7, dorsal views of abdomen to show gut coiling *in situ*; 8, gut dissected and uncoiled; 9, crop with 'bursters' and proventriculus [bar, 0.5 mm: top left, mandibles; 1 mm: bottom left, abdomens and uncoiled gut; bottom middle, crop and proventriculus]. Abbreviations in Figs 1 and 2 indicate standard measurements (see text).



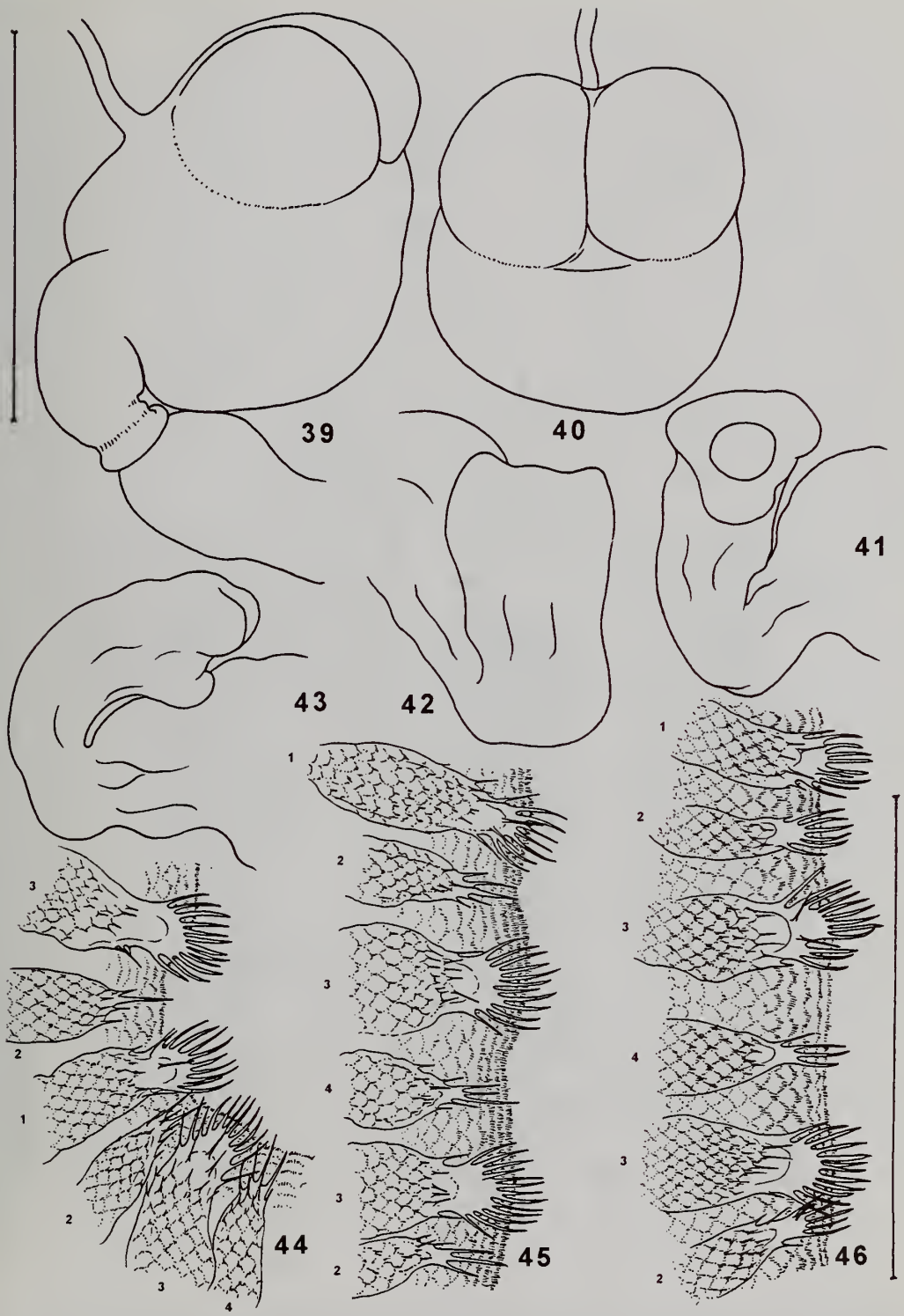

**Figs 10–15.** *Amicotermes autothysius.* 10–12, enteric valve seating and part of P3; 13–15, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 1 mm: middle, valve seating; 0.5 mm: bottom right valve armature].



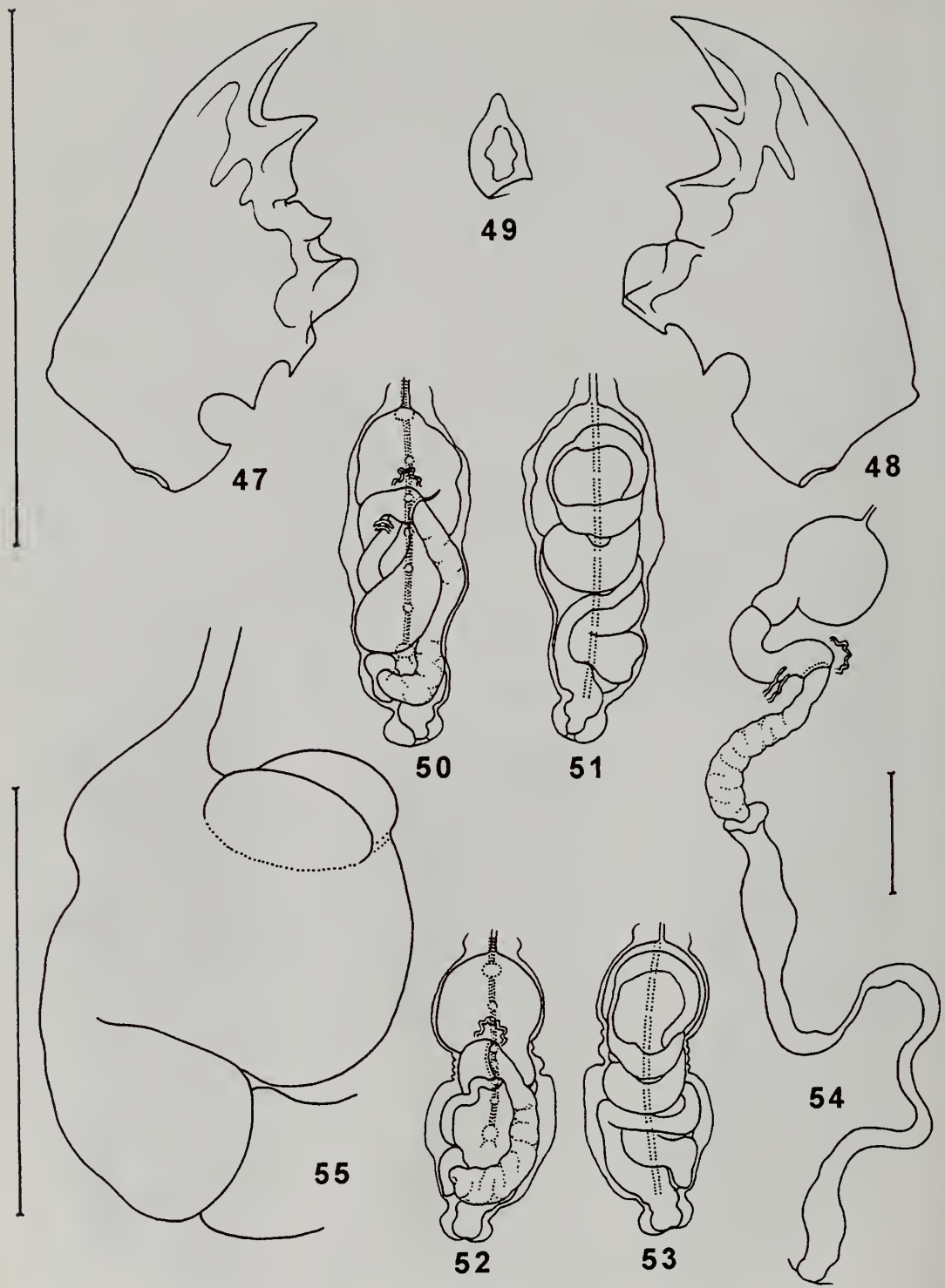

**Figs 16–28.** *Amicotermes camerunensis.* 16–18, mandibles with surface view of right molar plate; 19, 21, ventral and 22, 24, dorsal views of abdomen to show gut coiling *in situ*; 23, gut dissected and uncoiled; 24, crop with 'bursters' and proventriculus; 25–27, enteric valve seating and part of P3; 28, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: bottom right, abdomens and uncoiled gut; bottom middle, valve seating and crop].



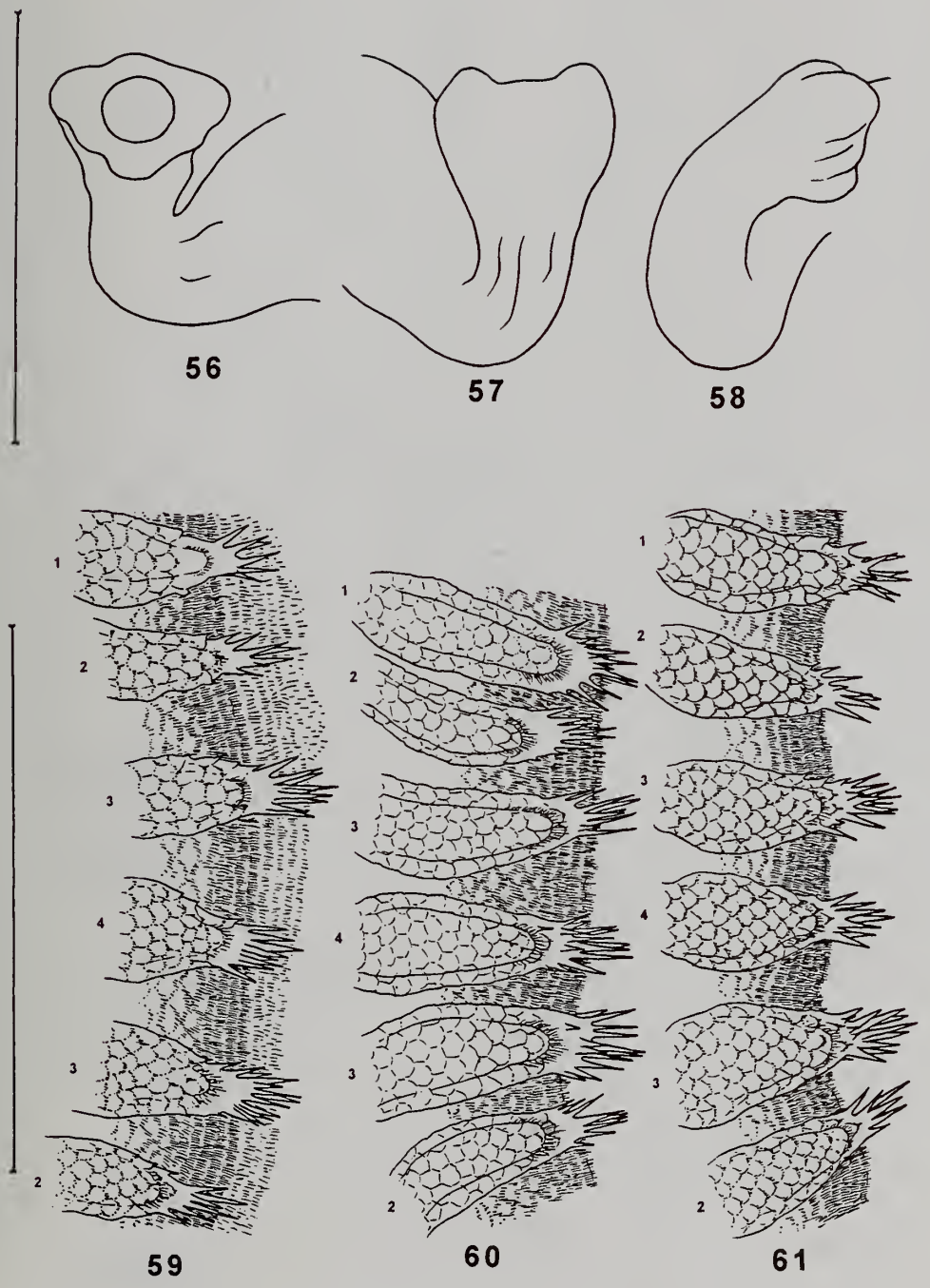

**Figs 29–38.** *Amicotermes congoensis*. 29–31, mandibles with surface view of right molar plate; 32, 34, 36, ventral and 33, 35, 37, dorsal views of abdomen to show gut coiling *in situ*; 38, gut dissected and uncoiled [bar, 0.5 mm: top left, mandibles; 1 mm: bottom middle, abdomens and uncoiled gut].



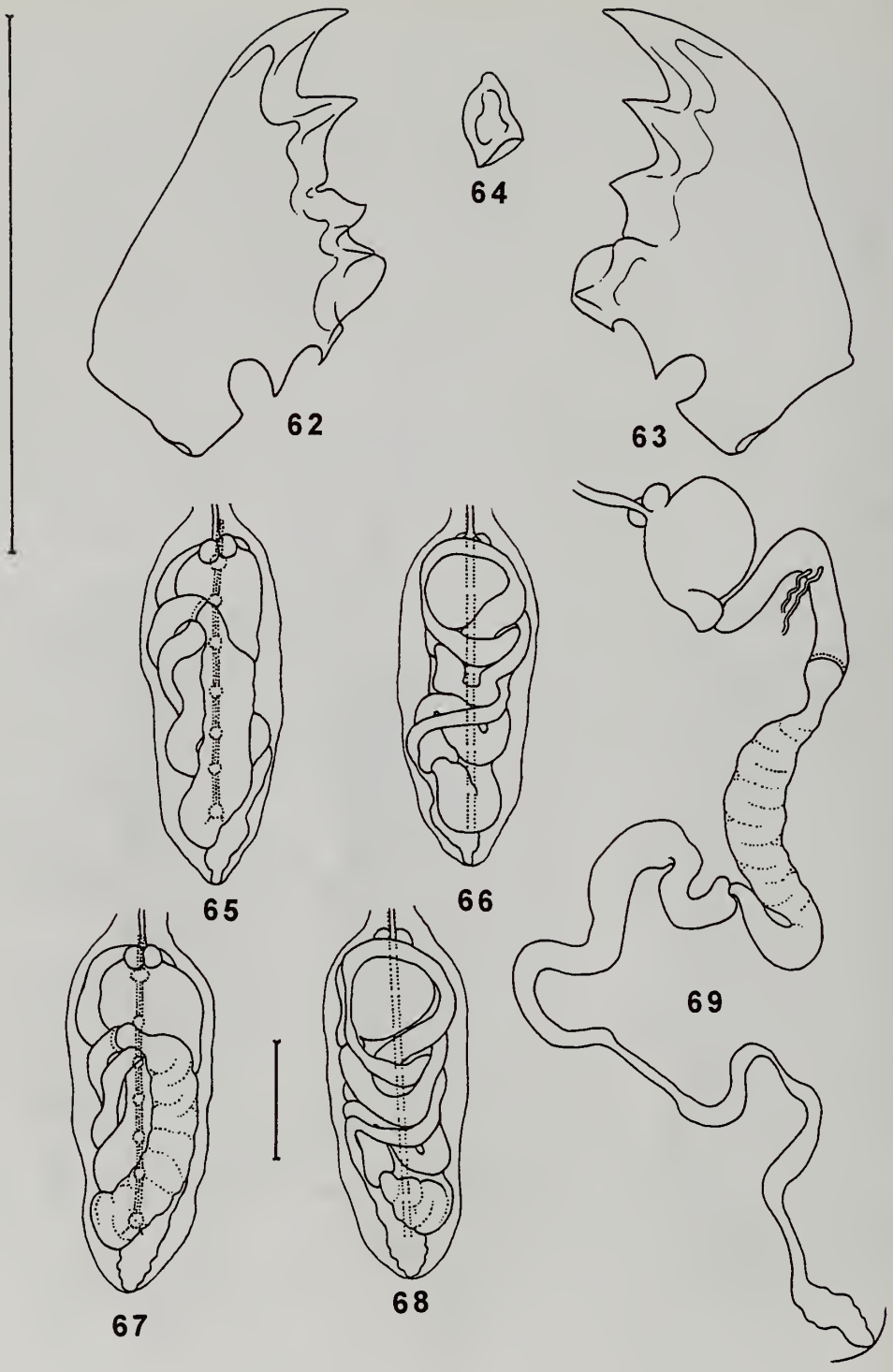

**Figs 39–46.** *Amicotermes congoensis*. 39–40, crop with 'bursters' and proventriculus; 41–43, enteric valve seating and part of P3; 44–46, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 1 mm: top left, crop and valve seating; 0.5 mm: bottom right valve armature].



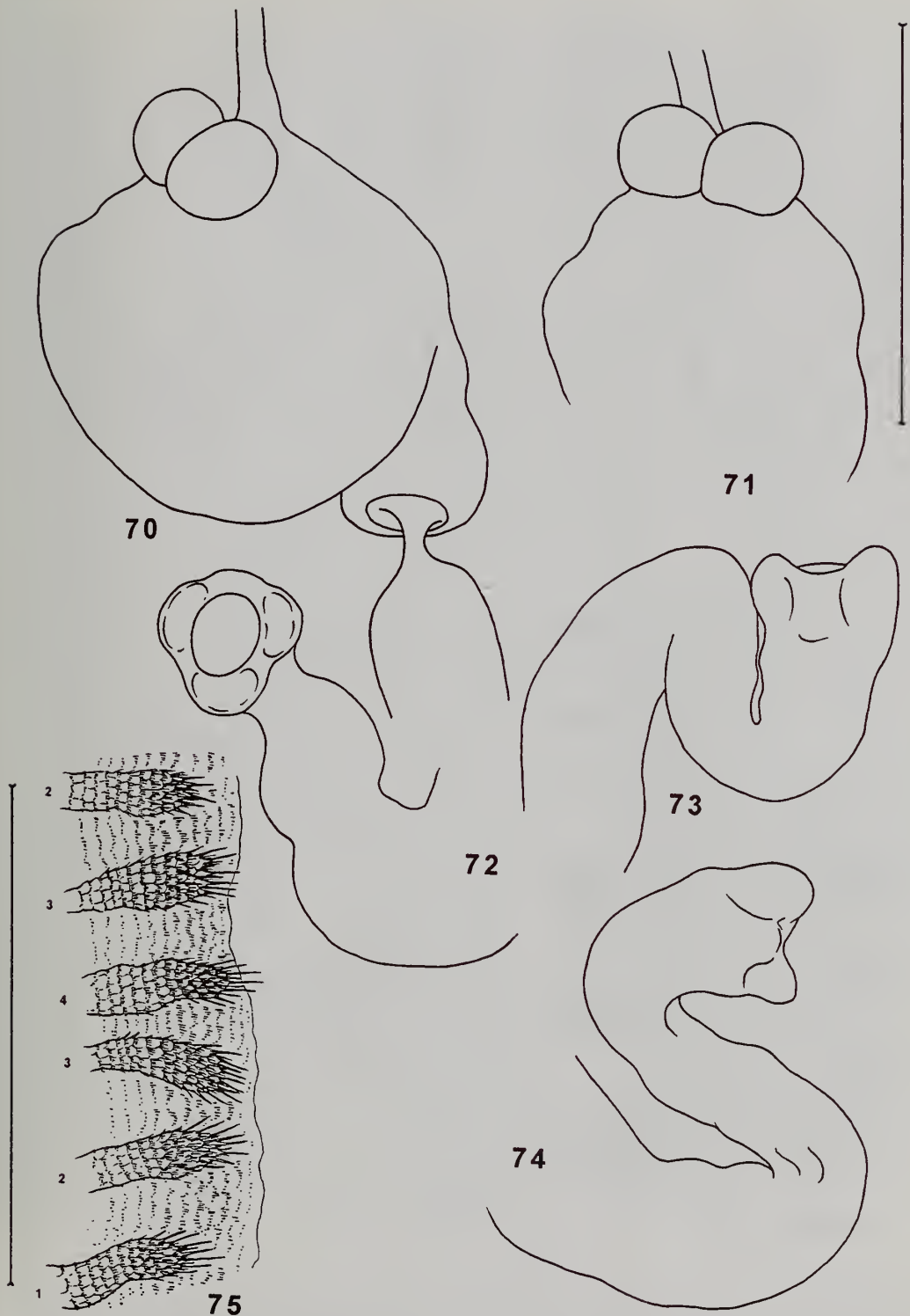

**Figs 47–55.** *Amicotermes cristatus.* 47–49, mandibles with surface view of right molar plate; 50, 52, ventral and 51, 53, dorsal views of abdomen to show gut coiling *in situ*; 54, gut dissected and uncoiled; 55, crop with 'bursters' and proventriculus [bar, 0.5 mm: top left, mandibles; 1 mm: bottom right, abdomens and uncoiled gut; bottom left, crop and proventriculus].



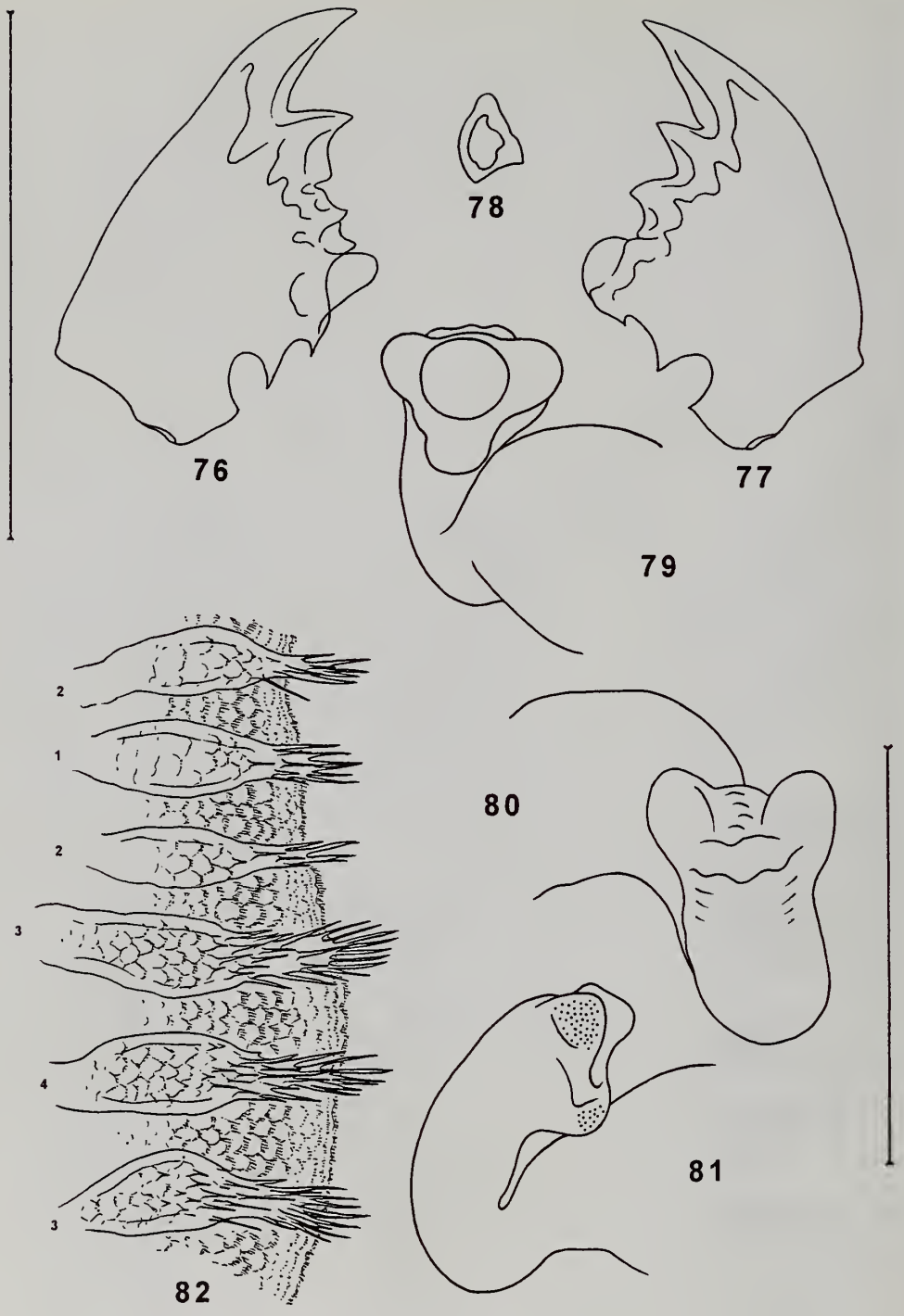

**Figs 56–61.** *Amicotermes cristatus*. 56–58, enteric valve seating and part of P3; 59–61, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 1 mm: top left, valve seating; 0.5 mm: bottom left valve armature].



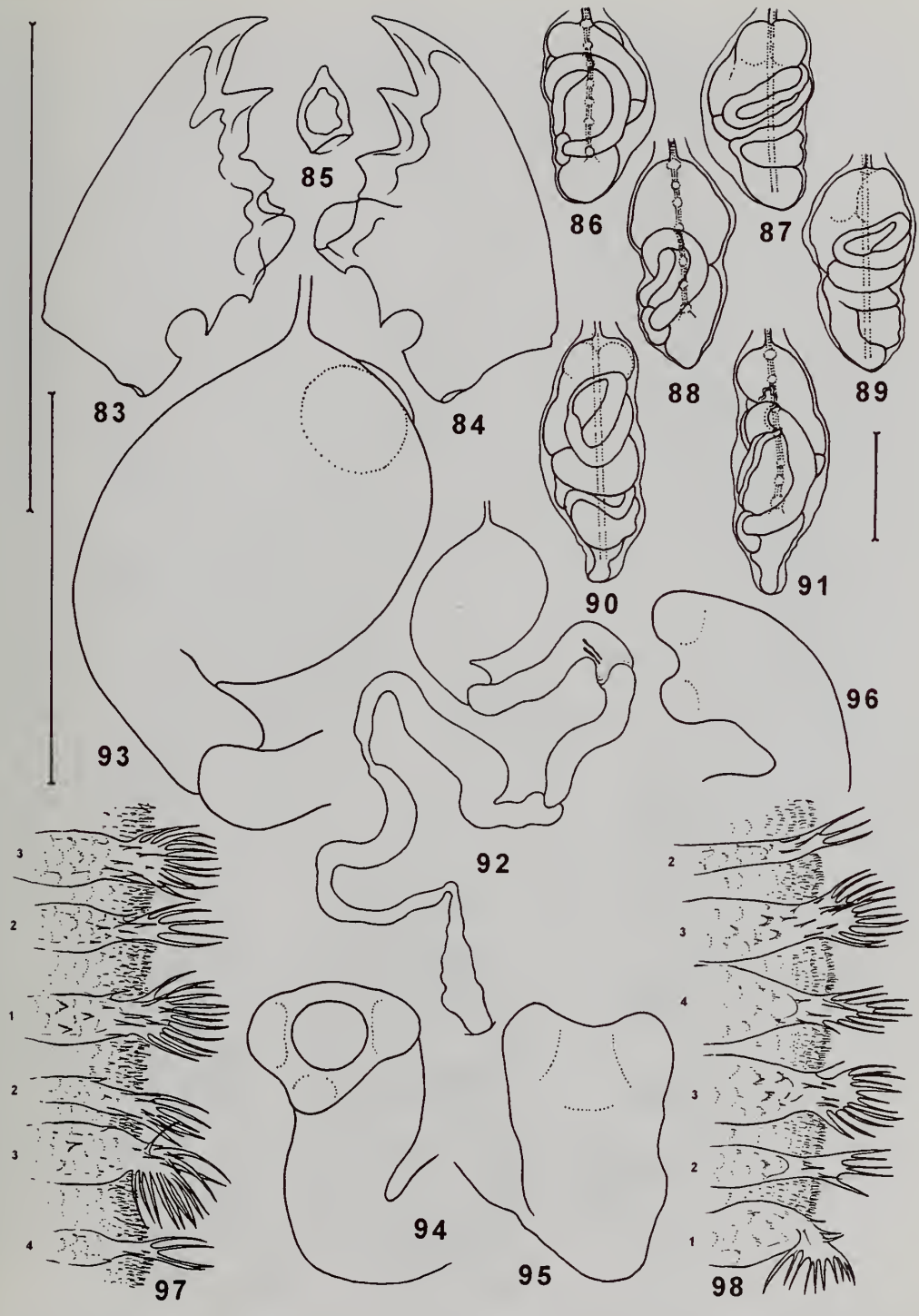

**Figs 62–69.** *Amicotermes dibogi.* 62–64, mandibles with surface view of right molar plate; 66, 67, ventral and 66, 68, dorsal views of abdomen to show gut coiling *in situ*; 69, gut dissected and uncoiled [bar, 0.5 mm: top left, mandibles; 1 mm: bottom middle, abdomens and uncoiled gut].



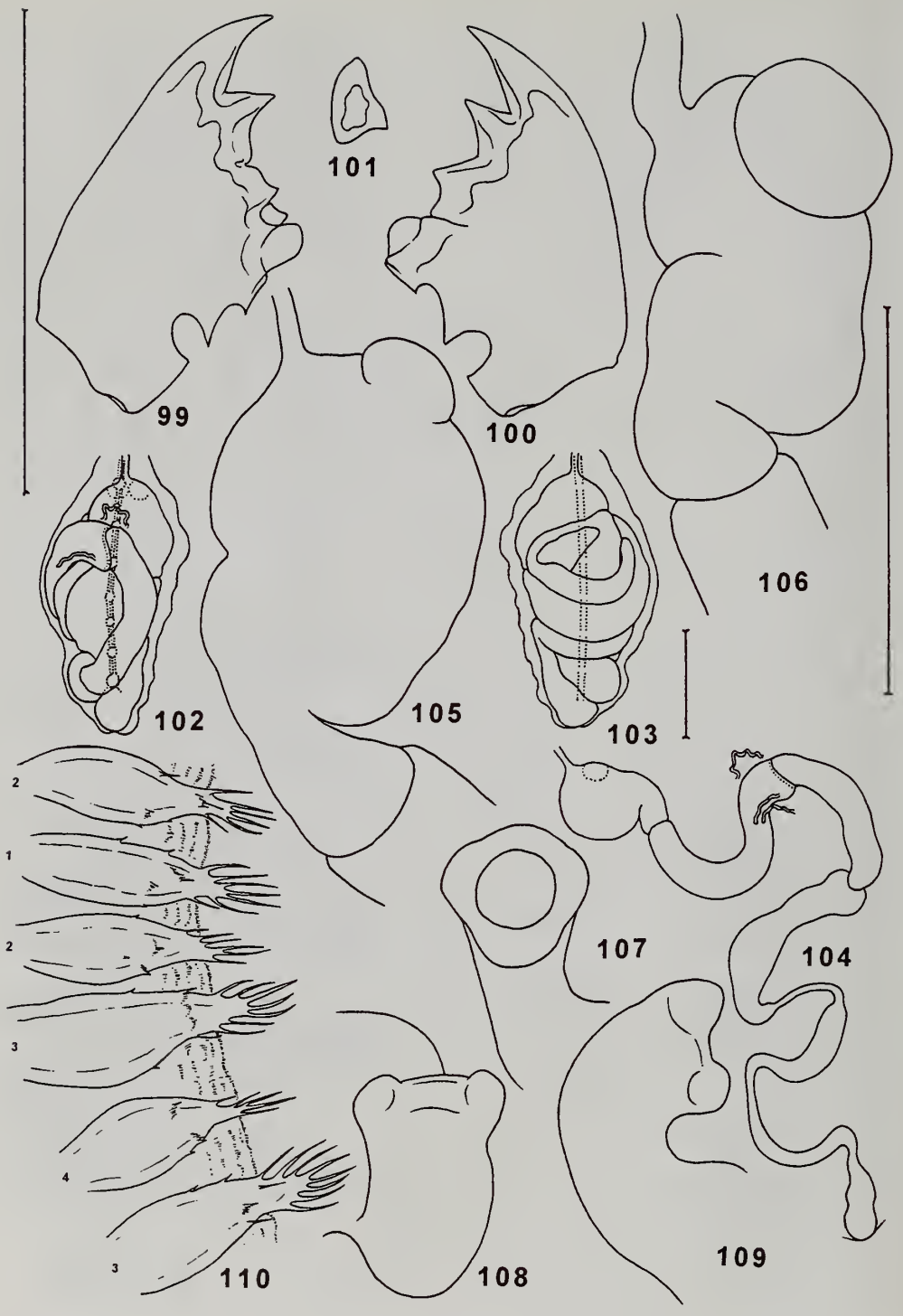

**Figs 70–75.** *Amicotermes dibogi*. 70, 71, crop with 'bursters' and proventriculus; 72–74, enteric valve seating and part of P3; 75, enteric valve armature opened out to show detail, ridge positions numbered [bar, 1 mm: top right, crop and valve seating; 0.5 mm: bottom left valve armature].



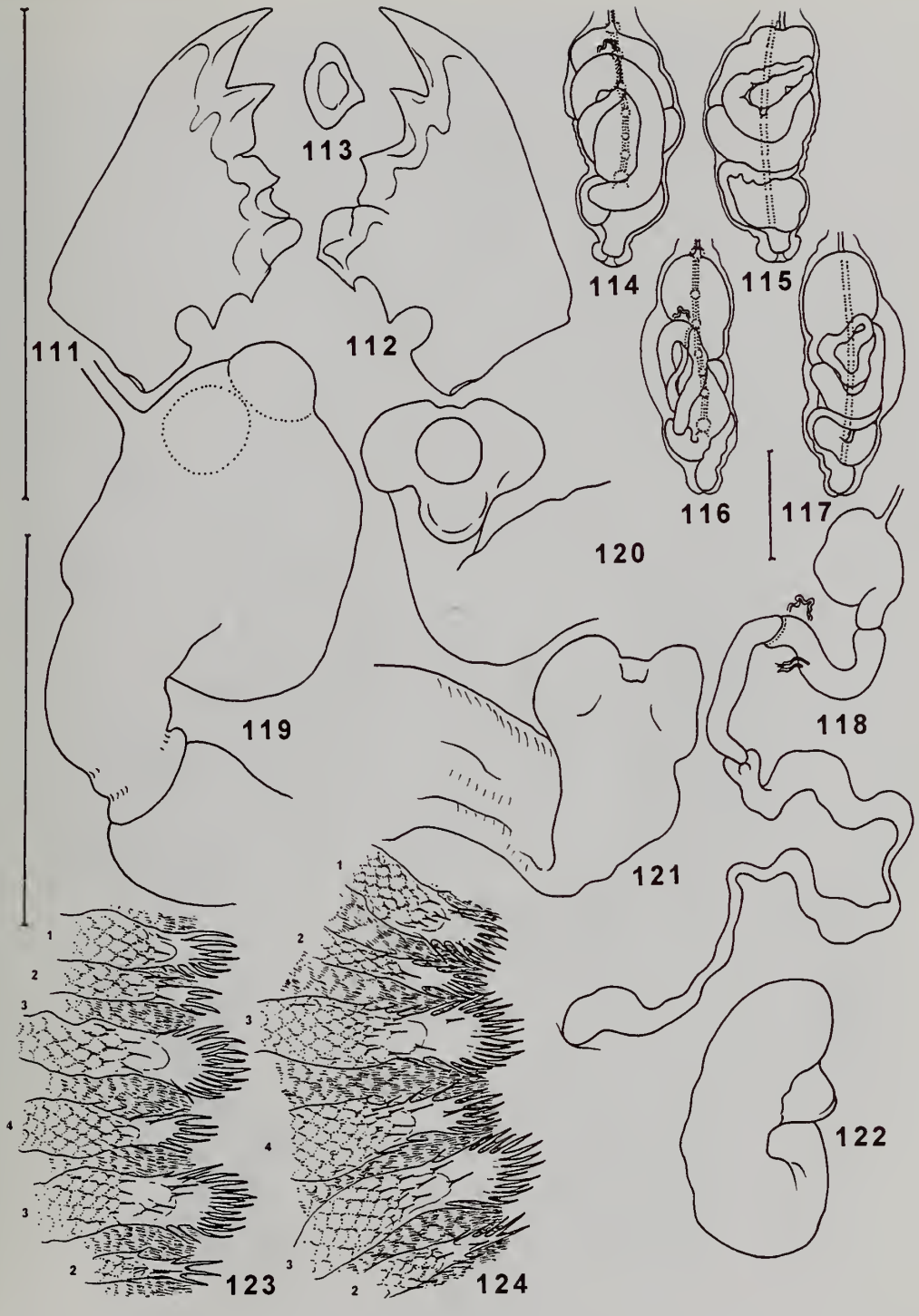

**Figs 76–82.** *Amicotermes galenus*. 76–78, mandibles with surface view of right molar plate; 79–81, enteric valve seating and part of P3; 82, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: bottom right, valve seating].



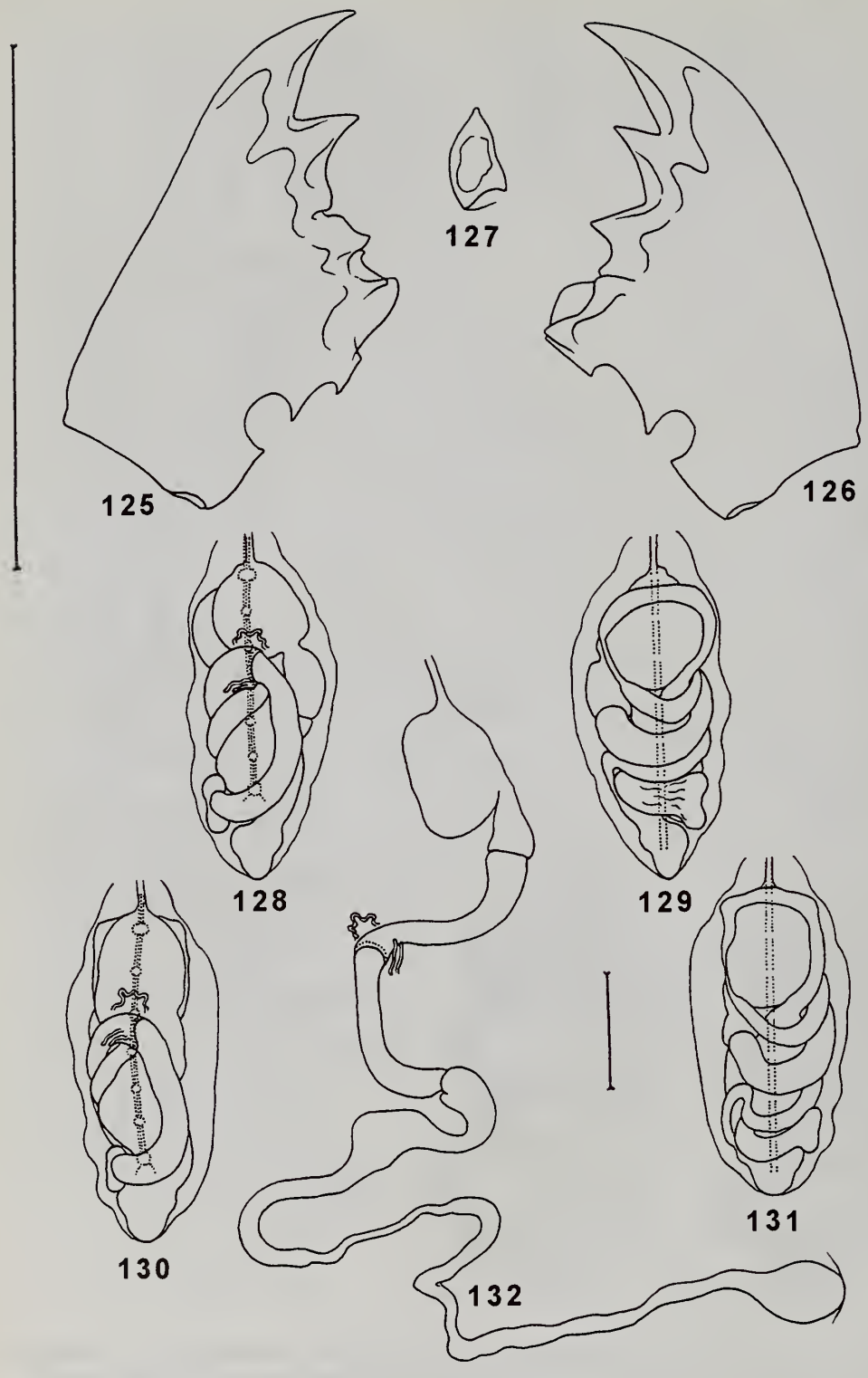

**Figs 83–98.** *Amicotermes gasteruptus*. 83–85, mandibles with surface view of right molar plate; 86, 88, 90, ventral and 87, 89, 91, dorsal views of abdomen to show gut coiling *in situ*; 92, gut dissected and uncoiled; 93, crop with 'bursters' and proventriculus; 94–96, enteric valve seating and part of P3; 97, 98, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: middle left, valve seating and crop; middle right, abdomens and uncoiled gut].



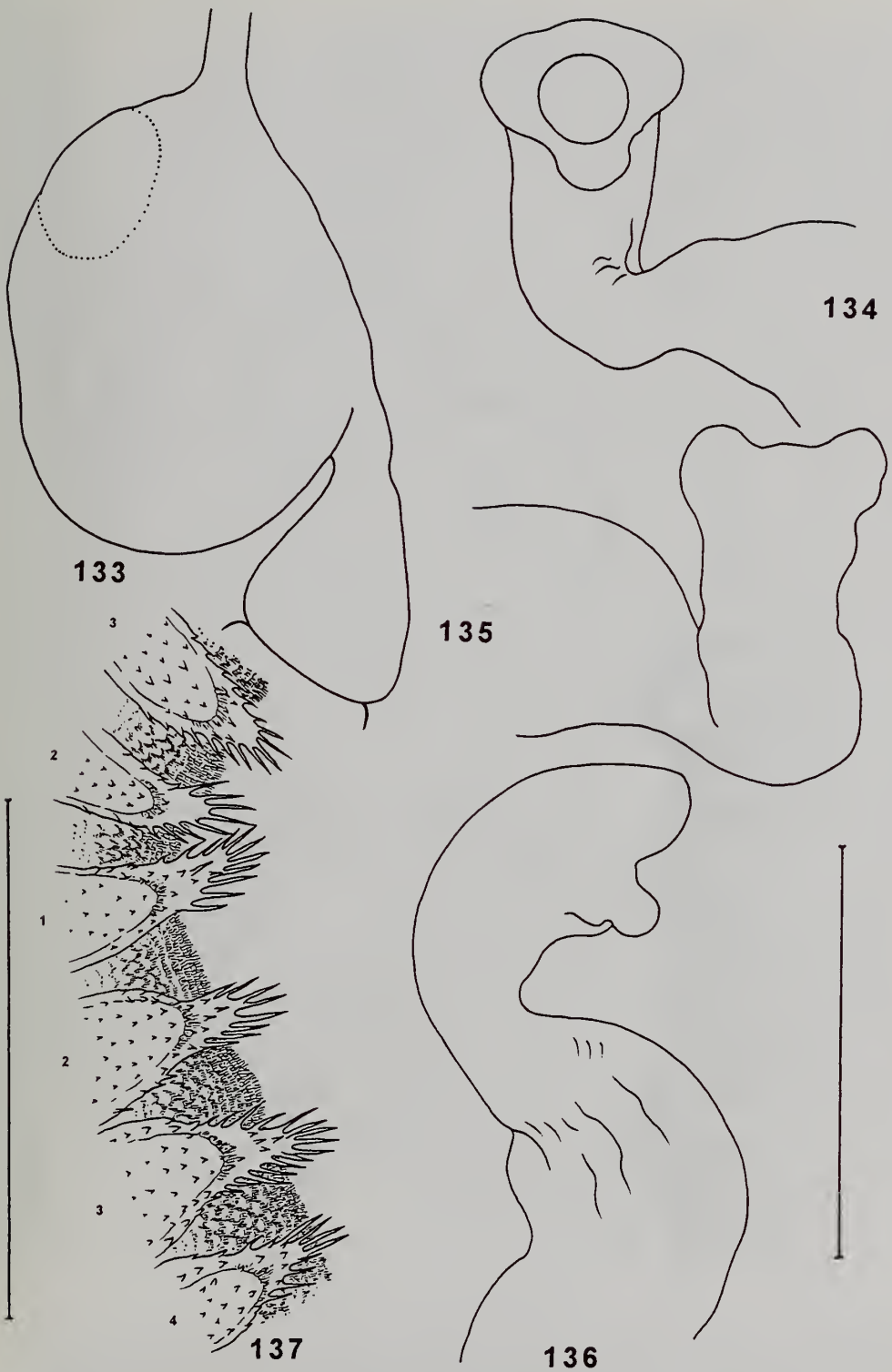

**Figs 99–110.** *Amicotermes ivorensis*. 99–101, mandibles with surface view of right molar plate; 102, ventral and 103, dorsal views of abdomen to show gut coiling *in situ*; 104, gut dissected and uncoiled; 105, 106, crop with 'bursters' and proventriculus; 107–109, enteric valve seating and part of P3; 110, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: middle right, abdomens and uncoiled gut; top right, valve seating and crop].



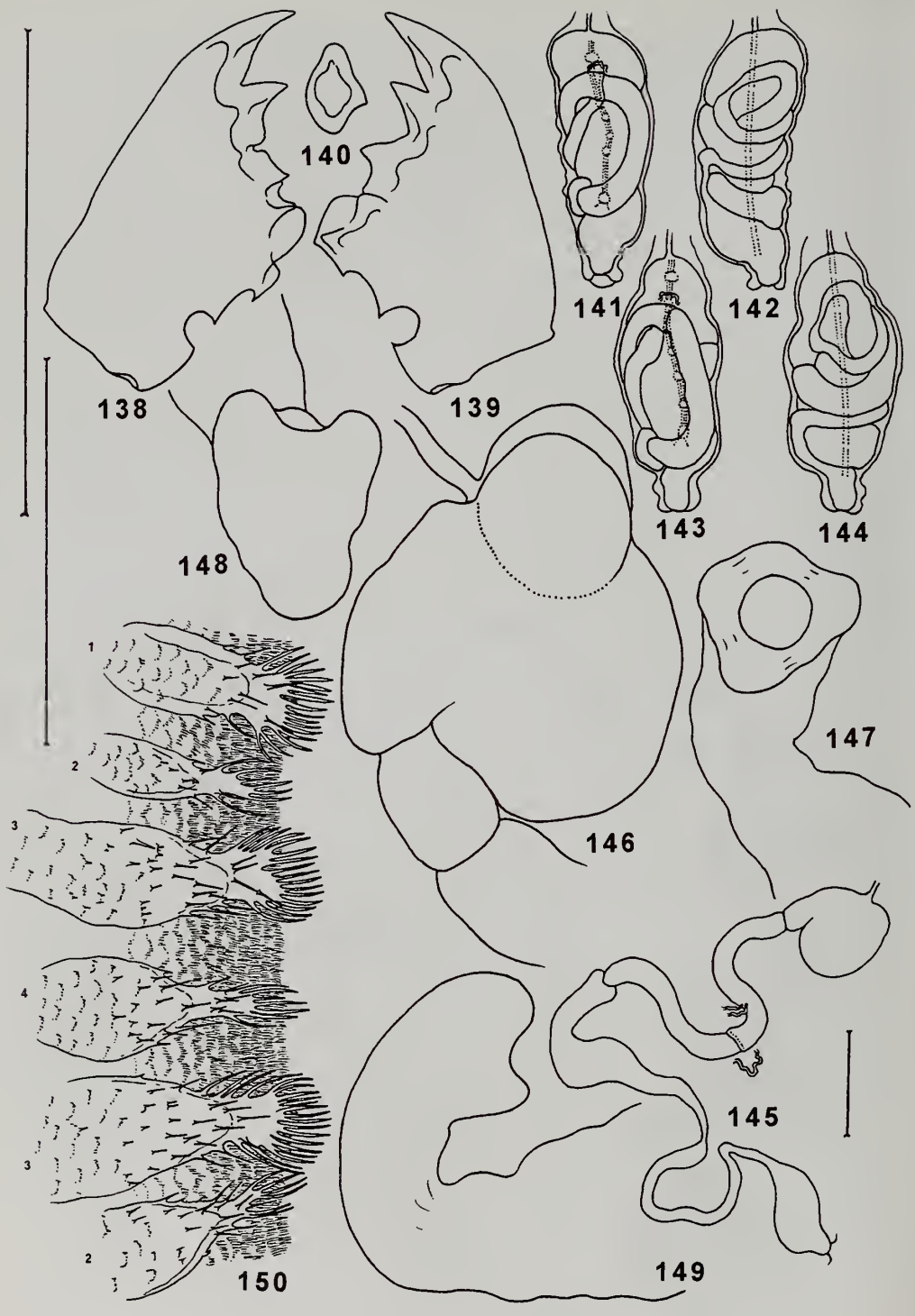

**Figs 111–124.** *Amicotermes mayombei.* 111–113, mandibles with surface view of right molar plate; 114, 116 ventral and 115, 117, dorsal views of abdomen to show gut coiling *in situ*; 118, gut dissected and uncoiled; 119, crop with 'bursters' and proventriculus; 120–122, enteric valve seating and part of P3; 123, 124, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: middle right, abdomens and uncoiled gut; middle left, valve seating and crop].



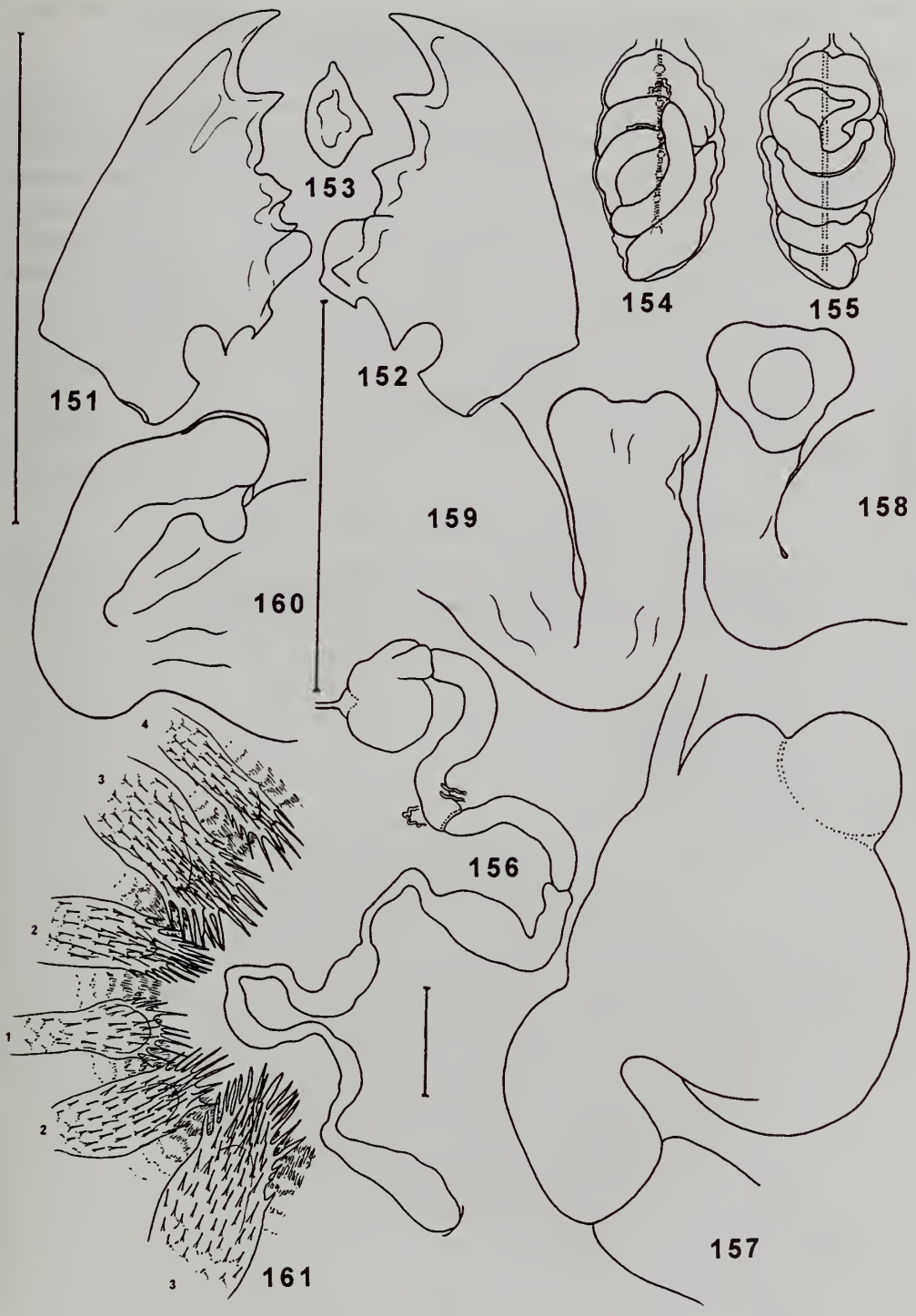

**Figs 125–132.** *Amicotermes mbalmayoensis.* 125–127, mandibles with surface view of right molar plate; 128, 130, ventral and 129, 131, dorsal views of abdomen to show gut coiling *in situ*; 132, gut dissected and uncoiled [bar, 0.5 mm: top left, mandibles; 1 mm: bottom middle, abdomens and uncoiled gut].



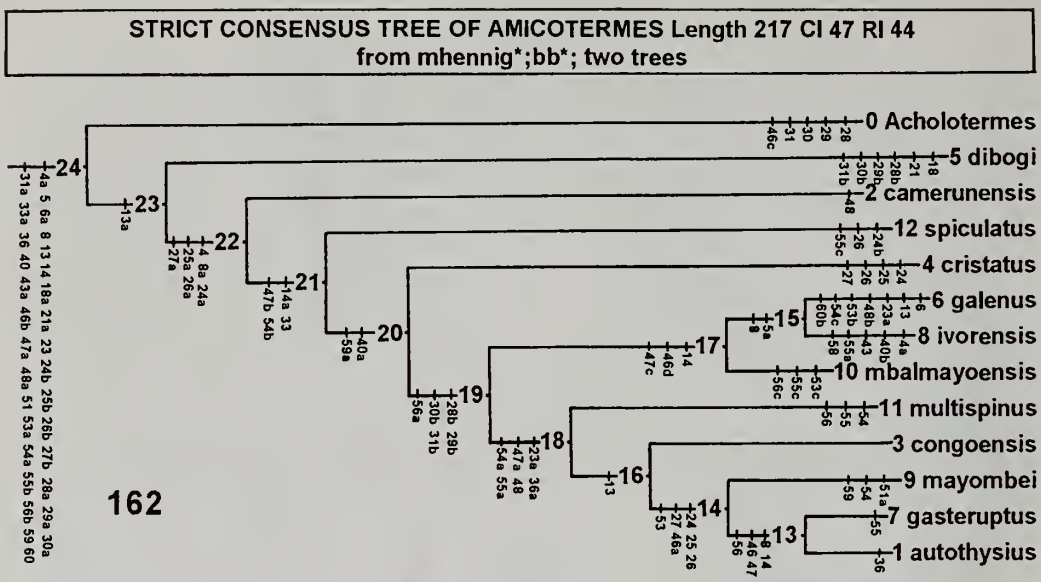

**Figs 133–137.** *Amicotermes mbalmayoensis.* 133, crop with 'bursters' and proventriculus; 134–136, enteric valve seating and part of P3; 137, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: bottom left, valve armature; 1 mm: bottom right, crop and valve seating;].

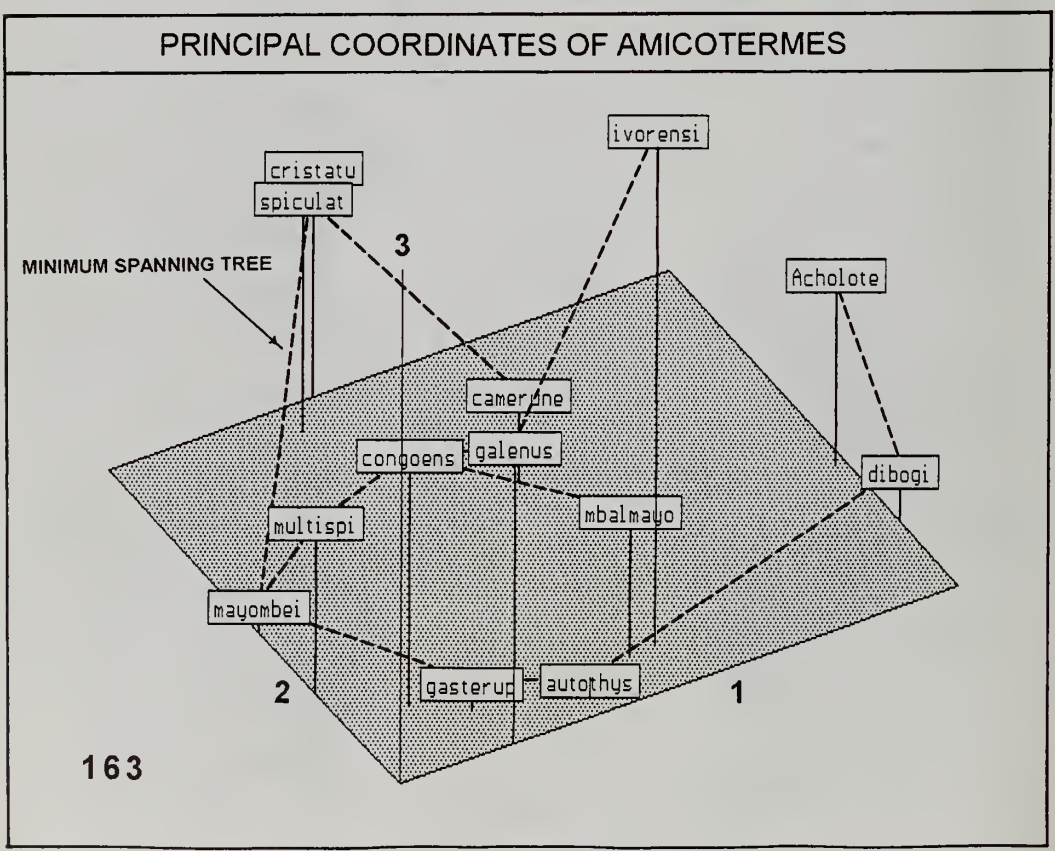



**Figs 138–150.** *Amicotermes multispinus.* 138–140, mandibles with surface view of right molar plate; 141, 143 ventral and 142, 144, dorsal views of abdomen to show gut coiling *in situ*; 147, gut dissected and uncoiled; 146, crop with 'bursters' and proventriculus; 147–149, enteric valve seating and part of P3; 150, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: bottom right, abdomens and uncoiled gut; middle left, valve seating and crop].

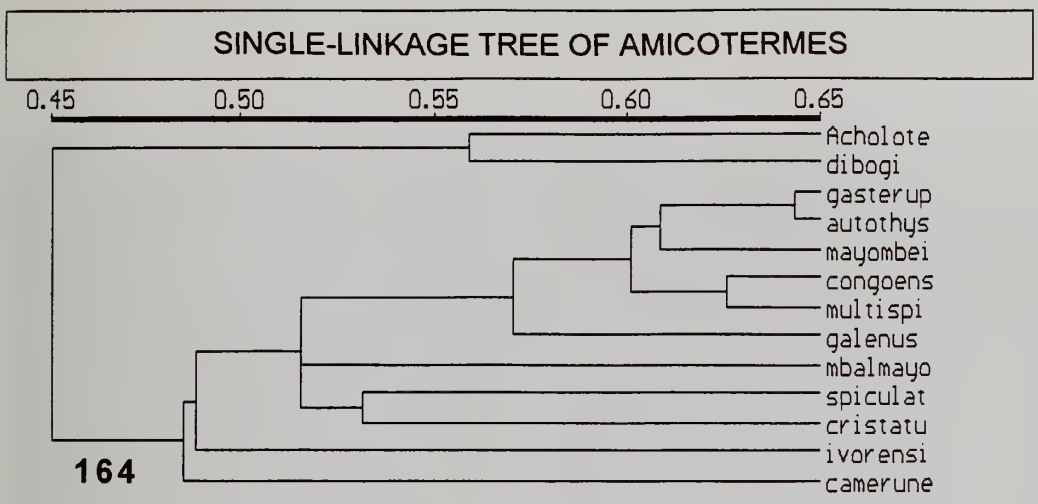


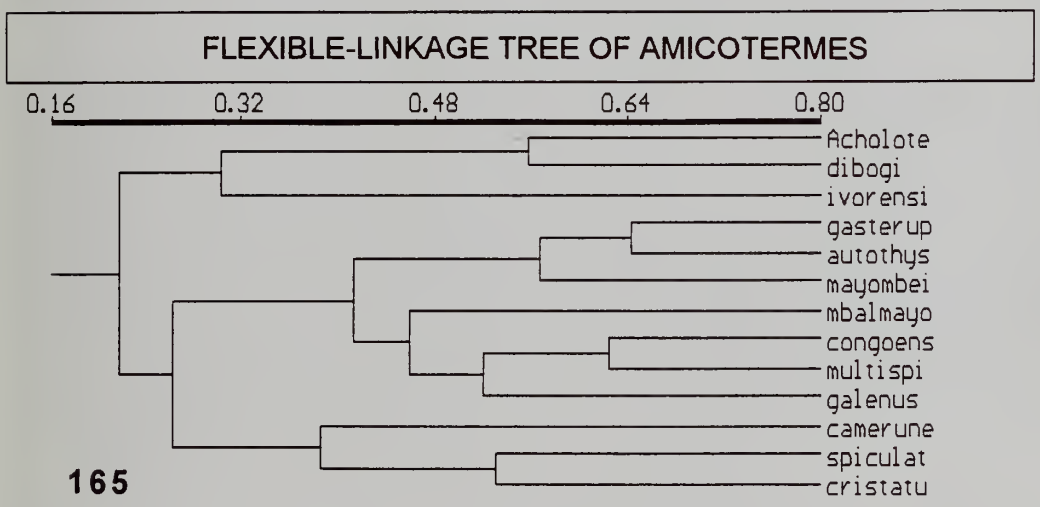

**Figs 151–161.** *Amicotermes spiculatus*. 151–153, mandibles with surface view of right molar plate; 154, ventral and 155, dorsal views of abdomen to show gut coiling *in situ*; 156, gut dissected and uncoiled; 157, crop with 'bursters' and proventriculus; 158–160, enteric valve seating and part of P3; 161, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: bottom right, abdomens and uncoiled gut; middle left, valve seating and crop].

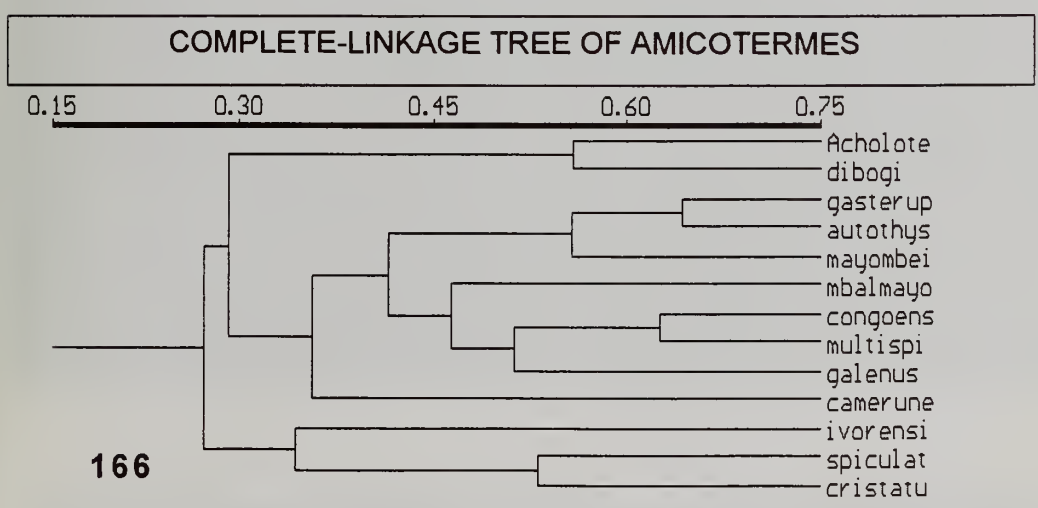


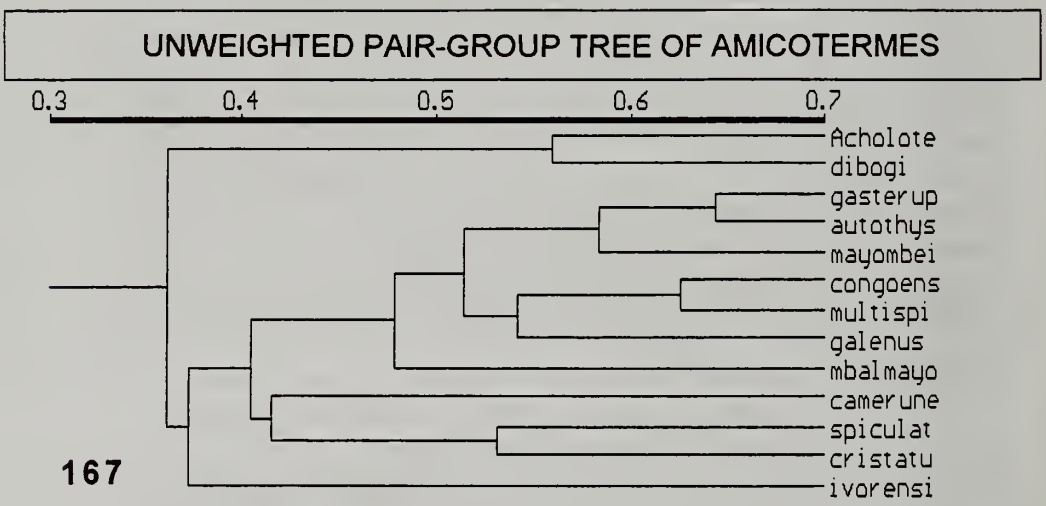

**Figs 162, 163.** *Amicotermes.* 162, Strict consensus tree from Hennig most parsimonious two trees, showing states of characters with retention indices >50 at each node and for individual taxa (states shown alphanumeric, 1, 1a, 1b . . . etc); 163, Principal coordinates plot of eigenvectors on coordinates 1, 2 & 3, with minimum spanning tree superimposed as a broken line.

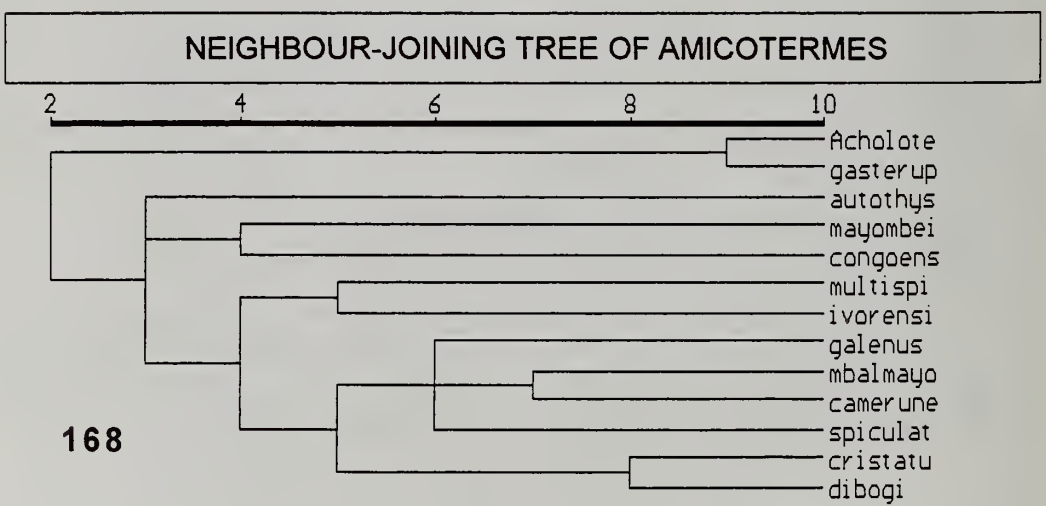


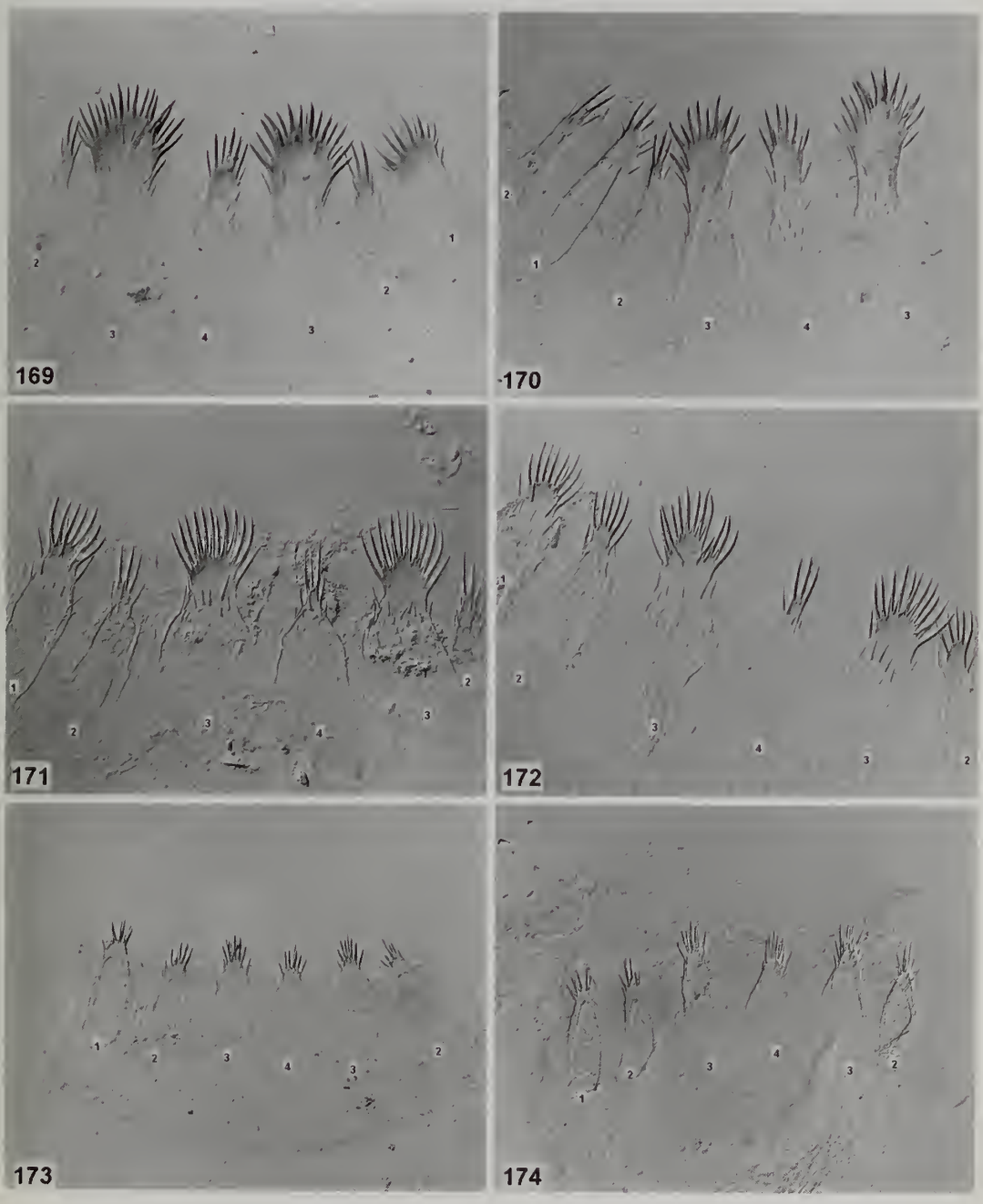




**Figs 164–166.** *Amicotermes,* phenetic trees. 164, Single Linkage tree; 165, Flexible Linkage tree; 166, Complete Linkage tree.

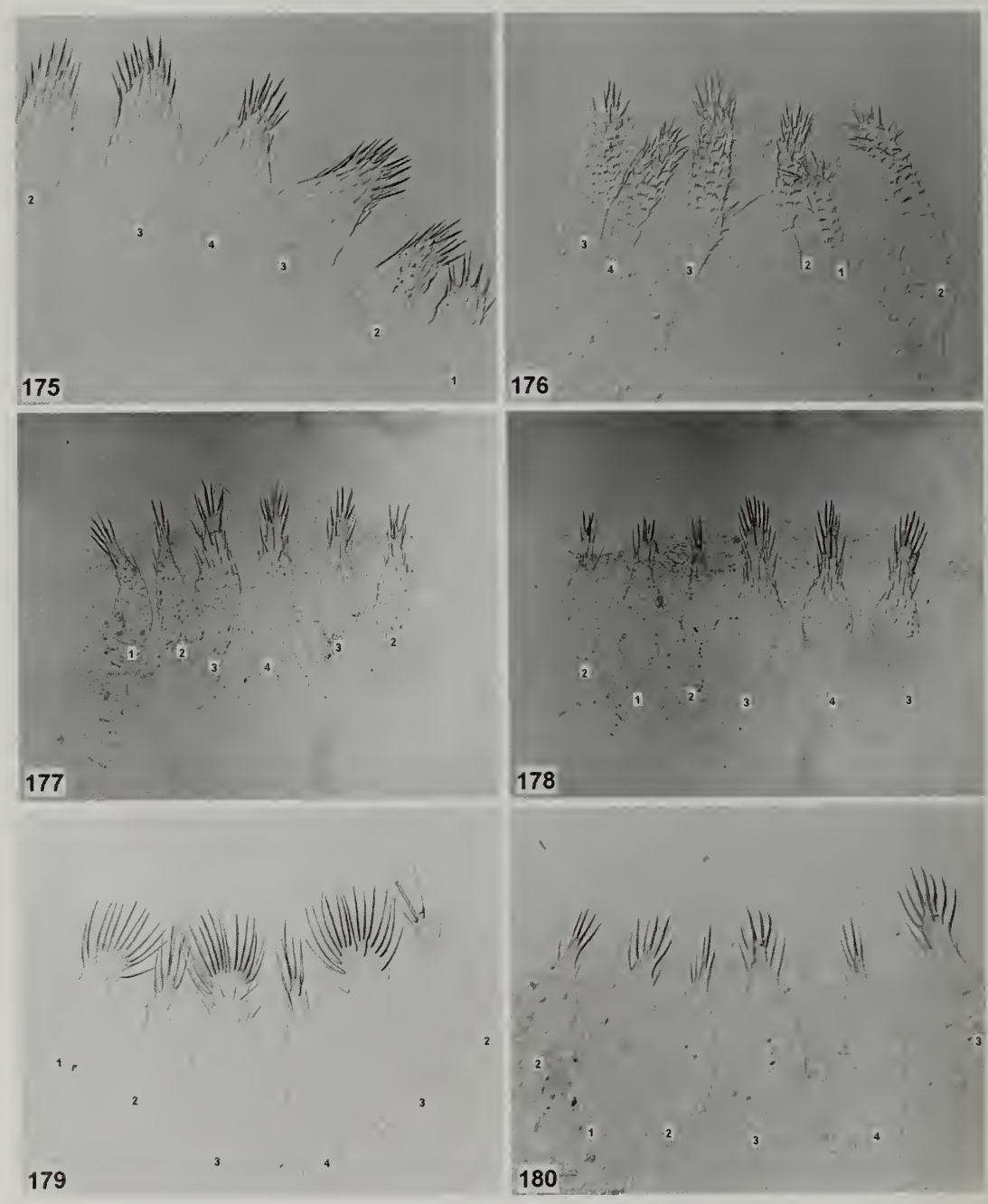


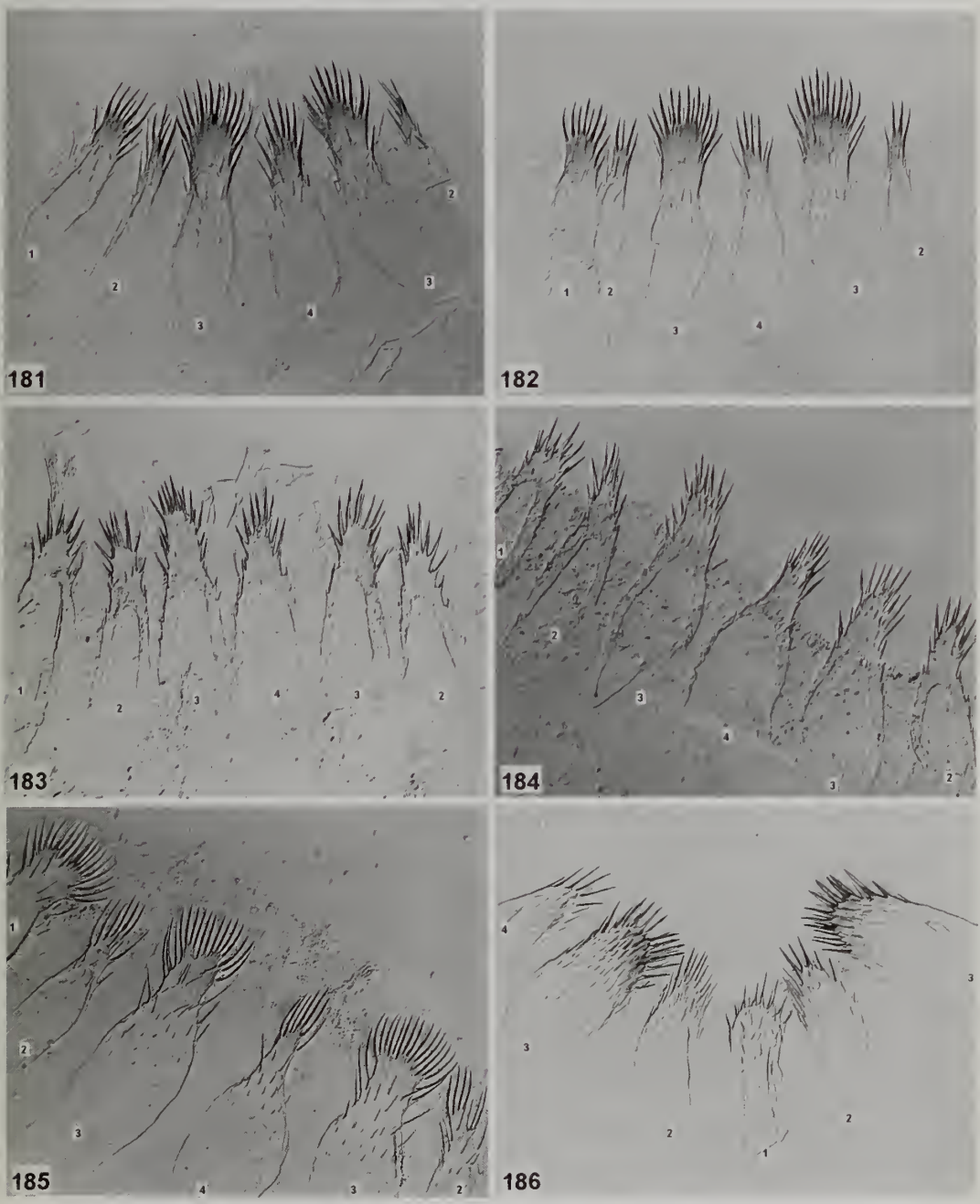

**Figs 167, 168.** *Amicotermes,* phenetic trees. 167, Unweighted Pair-Group Method of Averages tree; 168, Saitou and Nei Neighbour-joining tree.




**Figs 169–174.** *Amicotermes*, enteric valve armature, valves slit and opened out; 169, 170, *A. autothysius*; 171, 172, *A. congoensis*; 173, 174, *A. cristatus*.




**Figs 175–180.** *Amicotermes*, enteric valve armature, valves slit and opened out; 175, *A. camerunensis*; 176, *A.dibogi*; 177, 178, *A. galenus*; 179, *A. gasteruptus*; 180, *A. ivorensis*.




**Figs 181–186.** *Amicotermes*, enteric valve armature, valves slit and opened out, 181, 182, *A. mayombei*; 183, 184, *A. mbalmayoensis*; 185, *A. multispinus*; 186, *A. spiculatus*.